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Effects of Urbanization on Assemblages of Ground Beetles (Insecta: Coleoptera: Carabidae) in Central Alberta, Canada

by

Dustin Joseph Hartley

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology

Department of Biological Sciences

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ABSTRACT

Carabid beetle assemblages, as sampled by pitfall trapping along an urban-rural gradient in central Alberta, were quantified and analyzed in aspen forest sites, grassland sites and graveyard sites in order to study relationships between urbanization and assemblage structure of these insects. Urbanization significantly affected assemblage diversity and density as estimated by activity in all habitats. In aspen forests, populations of non-native species were scrutinized to determine their effect on native carabid assemblages. The progress of an invasion by a single exotic species (*Pterostichus melanarius* Illiger) was also assessed in relation to data from previous studies. Comparisons were made between grassland and graveyard sites to determine the relative contributions of landscape and habitat quality to assemblage attributes. Graveyards were used to establish the expectations of landscape effects as they were similar along the gradient in habitat quality. Landscape effects were more numerous than habitat quality effects in grassland assemblages.

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Dedication

To my family, friends, and supervisors who stood by me and believed in me during the most difficult time in my life. Thank you so much. We all knew I could do this.

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CHAPTER ONE

INTRODUCTION

Urbanization is a dominant global trend. The United States Bureau of Census defines urban areas as those with human populations greater than 186 persons/km^2 Pickett et al. 2001). Presently around the world less than half of the human population lives in urban areas but this is projected to rise to 60% in the next 30 years (United Nations 1993). This means that a great deal of agricultural land and natural habitat will be "urbanized". In addition to increased human habitation, urbanization in North America is associated with an increase in energy consumption and extensive landscape modification (McDonnell and Pickett 1990). Within some distinct ecological regions (e.g. Puget Sound Lowlands, British Columbia Lower Mainland, Great Lakes Forest) a significant proportion of the area has already been converted to urban landscape. In the interests of conservation of biodiversity, there is a need now to understand the effects of urbanization on the biota living within and around cities.

Urbanization involves changes in: 1) disturbance regimes; 2) biota, including introduced organisms; 3) landscape structure; and 4) pollution and other physiological stresses for organisms. These changes take place on a scale much greater than an ecologist can study experimentally. Therefore, urban-rural landscape gradients provide an exceptional template for the study of the effects of environmental change.

1.1 URBAN ENVIRONMENTS

Cities and surrounding urban areas, are a mosaic of different habitats, which range from biotically sterile concrete and asphalt areas to intensely managed vegetation (parks, yards, gardens, cemeteries, etc.), to relatively undisturbed areas

(unmanaged woodland, vacant lots, ponds, streams, rivers, etc.), or "greenspaces" in the jargon of the conservation movement. Greenspaces are essential not only to the quality of life for urban residents, but as refuges for plants and animals, and as filters for by-products of urban life. The maintenance of biodiversity, an indicator of ecosystem integrity (Heliövaara and Väisänen 1984), is key to having ecologically viable greenspaces extend into the future.

Urban environments support a high proportion of intentionally and accidentally introduced plant and animal species (McDonnell and Pickett 1990). These exotic species may have positive, negative, or neutral impacts on biological diversity in cities. Many species of ornamental and garden plants in urban backyards actually have a positive impact on the biodiversity of insects in urban areas (Davis 1978, Frankie and Ehler 1978). On the other hand, house cats, for an example toward the other outcome, have a negative impact on urban bird populations and communities (Churcher and Lawton 1987).

Cities act as point sources for the introduction of exotic species. Human activities are agents that allow introduced species to disperse to foreign habitats, either intentionally or accidentally [e.g., Cuban tree frogs in Florida, U.S.A., Menshaka (1996)]. The volume of products and goods shipped between countries is tremendous, and this allows transient individuals of many species to find their way to foreign cities. Cities provide the first habitats in which many newly introduced species must meet the challenges of life, where the immigrants either establish resident populations, or fail to do so. As the source areas of introduction, cities usually have larger populations of the exotic organisms than outlying areas. With

populations established in urban habitats, an immigrant species may or may not spread into the surrounding countryside.

1.2 EXOTIC SPECIES AND URBAN ENVIRONMENTS

The ability of an exotic species to invade, establish and spread is thought to reflect the action of extrinsic or intrinsic factors. Those ecologists supporting the crucial importance of extrinsic factors in population processes postulate that the local community determines the success of an invader. Systems with high diversity and few empty niches (or low average niche width) are referred to as saturated, and an exotic species is thought to be unlikely to establish and spread in such systems (Moyle 1986). Urban habitats, however, seem to be unsaturated, exhibiting "low biotic resistance", and may thus be more subject to entry by invaders than are the surrounding rural habitats. Thus, urban habitats become the main home to exotic species that cannot compete in more natural habitats.

Ecologists supporting the crucial importance of intrinsic factors for population growth and expansion postulate that the characteristics of the invader determine colonization success or failure, and that the issue of saturation is irrelevant (Simberloff 1986). According to the 'intrinsic control' postulate, urban habitats are not subject to invasion because they are unsaturated; rather, they are just invaded more often and, perhaps, the biological features of the invaders better match the opportunities available in urban areas than do the biological features of native species (Spence 1990). Support is available for both hypotheses, and it is likely that a combination of extrinsic and intrinsic properties are required to explain relative success of invading species.

Five intrinsic properties seem to be crucial or "key" for a species to be a superior invader. First, the ability for a population to persist at low numbers is key in the initial phase of introduction. Second, success at finding a mate at low densities while adjusting to local conditions is also vital during the initial phase of colonization. Third, flexibility in diet is important because the food supply in the new situation is unlikely to be the same as it was in the place of origin. A fourth key characteristic is high reproductive capacity. If the invading members of a species propagate quickly, its invading population is more likely to survive unfavourable vicissitudes of the new environment. The fifth key characteristic is the ability to disperse. Coupled with high reproductive capacity this may be the defining characteristic that separates superior invaders from those that merely establish a population. Greater dispersal power allows a greater amount of habitat to be exploited, and increases the chances of finding optimal situations for new populations.

1.3 METHODS OF STUDY

One way to study the effects of urbanization on a biota is to use a comparative method, applied to a moderately diverse taxon whose members are readily obtained and easily identified. The use of a landscape gradient allows one to compare assemblages of the chosen taxon in habitats ranging from rural to urban, with the rural end providing species assemblages most similar to those that originally occupied the now-urbanized area. The gradient paradigm is based on the assumption that "environmental variation is ordered in space, and that spatial patterns govern the corresponding structure and function of ecological systems" (McDonnell and Pickett

1990). Simply put, if we take a tract of land, that varies consistently as a gradient (in one characteristic of the landscape), and measure features of a group of organisms along that transect we can attribute changes in that group that show a graded response to the feature that varies along the gradient. Therefore, by sampling assemblages of the selected taxon at different points on a gradient that moves from densely urban to agricultural and to undeveloped natural habitat, graded patterns of response in the characteristics of the assemblages can be reasonably attributed to the amount of urbanization.

Using a landscape gradient we can identify effects of urbanization on the selected taxon, and also study the patterns of dispersal of introduced members of that taxon on a landscape scale. With the use of multiple habitats we may even begin to recognize what patterns in the assemblages are due to landscape effects and what patterns are associated with differences in habitat quality.

In the following thesis I have studied carabid beetles on an urban-rural gradient in the vicinity of Edmonton, Alberta, Canada. I have used pitfall traps to collect carabids from replicated sites in deciduous forest, grassland and graveyard habitats in urban, suburban and rural areas.

1.4 CARABID BEETLES AND URBANIZATION

Carabid beetles are excellent model organisms to study the effects of urbanization, as well as the effects of introduced species. Carabids are abundant in urban habitats, including a suite of introduced species (Spence and Spence 1988). Many are predators of macro-invertebrates (Lindroth 1961-1969). They are sensitive to habitat variation, comparatively well known taxonomically, and easy to collect

(Niemelä 1996). A wide variety of habitats are occupied by various species, including forest litter and grassland, which are especially important in the context of urban habitats.

Carabids, while being a diverse taxon worldwide (more than 40,000 species (Erwin 1985)) and locally (approximately 400 species in Alberta), are for the most part similar in form. While some groups exhibit adaptations for burrowing, tree dwelling, cave dwelling, swimming, etc. (Evans 1990) the bulk of carabid adults share a body plan or morphology for running and pushing, like a wedge, under materials. Mouthparts exhibit a similar pattern: while some taxa are characterized by special modifications, such as those for capturing and eating particular groups of macro-invertebrates, adults of most taxa have rather generalized structures for obtaining and eating particulate matter.

Carabids are holometabolous insects. Members of most species complete their life cycle (egg to adult) in one year, and perish; adults of some taxa live as long as 4 years (Lövei and Sunderland 1996). Most Nearctic carabids overwinter as adults and remain mainly inactive over the winter. Carabids are moderately fecund, with individual females usually producing hundreds of eggs (Den Boer and Van Dijk 1996), making them fine candidates for becoming established after introduction.

Because carabids are sensitive to changes in the environment they also appear to be selective of the microhabitats they inhabit (Niemelä and Spence 1994). While interspecific competition seems to have little effect on carabids (Lövei and Sunderland 1996), interactions with other predatory insects appear to affect microhabitat selection (Niemelä 1990).

Carabid dispersal is accomplished by walking or flying. Due to the high metabolic cost of development and maintenance of flight capability, some carabids have lost it (Nilsson et al. 1993), the mechanism of loss being mutation and selection. All adults of some species have the wings as very short stubs, or are actually totally wingless; these species, or individuals with reduced wings, are referred to as brachypterous. Further, some flightless species exhibit loss of thoracic flight muscles, with consequent reduction of the metathorax, and reduction of the elytral humeri. Some species are dimorphic, with individuals of two classes: brachypterous, with markedly reduced wings, and incapable of flight; and macropterous, with wings of normal size, and capable of flight. Most carabid species, however, have exclusively macropterous adults.

Carabid assemblages in the Edmonton area are known to contain introduced species. In 1990, the only exotic that was a major component of the assemblage was *Pterostichus melanarius* Illiger, a wing dimorphic species from Europe (Niemelä and Spence 1991). In Edmonton, populations *P. melanarius* were 20% macropterous, while populations 70 km away were 60-70% macropterous. This suggests that the populations were expanding away from Edmonton using flight to disperse (Niemelä and Spence 1991). There did not appear to be any negative effects on the native species of carabids.

1.5 GENERAL OBJECTIVES OF THE THESIS

This work was undertaken to meet the following objectives:

1) To determine the effects of urbanization on carabid beetles, using a landscape gradient in both grassland and deciduous forest habitats. Graded response

patterns in characteristics such as diversity were inferred to be responses of the carabid assemblage to urbanization. Two sets of analyses were conducted, one with introduced species and one without to determine the differing responses of native and introduced assemblages.

2) To observe temporal changes in the introduced carabid fauna. Based on trap catches, I determined if other introduced species have become major components of the fauna in urban areas and what, if any, changes have occurred in *P. melanarius* populations in relation to the populations of native species. Wing dimorphism frequencies were also determined to see if how spatially stable the populations of *P. melanarius* have become, in aspen forest, since the 1991 study by Niemelä and Spence.

3) To determine effects (negative or positive) of the introduced carabids on native carabids, 8-10 years after the 1991 study by Niemelä and Spence. Comparisons were made with the assemblages in 1991 and 1998-99 in aspen forest.

4) To determine what effects of urbanization on carabid assemblages are based on effects of landscape (external) differences and what effects are based on habitat quality (internal) differences. To do this, a habitat that does not vary in habitat quality was selected (graveyards) to serve as a baseline for establishing landscape effects, when compared to assemblages from more natural grasslands that showed significant local variation.

5) To determine if the assemblages of each of the habitat types were distinct from each other, and if they have a consistent core faunal. This refers mainly

to grassland and graveyard habitats. Ordinations of trap catch data were used to determine if the assemblages were distinct, both with and without introduced species.

CHAPTER TWO

CARABID BEETLES IN ASPEN FOREST ALONG AN URBAN-RURAL GRADIENT

2.1 INTRODUCTION

Urbanization involves increased human habitation of an area along with increased energy input and extensive landscape modification (McDonnell and Pickett 1990). Natural selection continues to act on species in the modified landscape, leading to adaptation in some, even those living in 'natural' areas left undeveloped in the city (Gill and Bonnet 1973, White and McDonnell 1988, McDonnell and Pickett 1990). In addition to providing novel selective pressures from physical effects, urban environments also place native species in regular contact with introduced taxa (e.g. Airola and Buchholz 1984, Niemelä and Spence 1991). Urbanization is generally associated with an increase in exotic species, be they plant or animal, and this is commonly linked with a negative impact on native biota (McDonnell and Pickett 1990).

Recent trends in ecosystem assessment involve defining bio-indicator groups, composed of species that are sensitive to changes in the local environment, and that provide a measurable responses to changes in the system. Human impacts in landscape ecology are commonly defined using landscape gradients (Ter Braak and Prentice 1988). The gradient paradigm postulates that environmental variation is ordered in space proportional to the extent of urbanization, and that the resulting patterns affect the structure and functional relations of the biota over the gradient (McDonnell and Pickett 1990). By measuring differences in the structure of the

chosen bio-indicator group, changes associated with the increasing intensity of the gradient type may be discovered, with the assumption that prior to the disturbance along the gradient (in this chapter, urbanization) the fauna was uniformly distributed.

I set out to study a northern assemblage of carabid beetles along an urban-rural landscape gradient extending some 45 km eastward from the downtown Edmonton, Alberta to outlying rural areas. The Holarctic ground beetles (Coleoptera, Carabidae) are primarily litter dwelling predators of macro-invertebrates (Lindroth 1969, p.XXXIII). Carabids are highly regarded as an indicator group because they are diverse, generally abundant, sensitive to habitat variation, known taxonomically adequately, and easy to collect (Spence et al. 1996). These features make them sensitive to change and relatively easy to work with.

Based on other gradient work, I began with two predictions. First, I predicted that the urban environment would be associated with lower diversity. This could reflect the loss of specialists and rare species because of habitat simplification (Davis 1978, Karr 1998). Second, I predicted that more introduced species would occur in urban areas as in previous studies of carabids and of other taxa (Airola and Buchholz 1984, Spence and Spence 1988, Niemelä and Spence 1991, Karr 1998).

2.2 MATERIALS AND METHODS

2.2.1 Materials

The study material obtained by pitfall trapping comprises a total of 21330 specimens representing 41 species, including 4 introduced species. Eight native species were common (> 5% of native species activity-density in one gradient position) and 29 native species were uncommon or rare (< 5% of native species

activity-density in one gradient position) (Table 2.2). Carabid adults were identified to species using the keys and descriptions provided by Lindroth (1961-69). However, generic names and specific epithets follow Bousquet and Larochelle (1993). Specimens were either pinned or stored in 70% ethanol. Voucher specimens were deposited in the E. H. Strickland Entomological Museum of the Department of Biological Sciences, University of Alberta.

2.2.2 Study Sites

During the summers of 1998 and 1999 my associates and I collected ground beetles using pitfall traps at specific sites along a landscape gradient extending from Edmonton, Alberta and surrounding area eastward roughly 45 km to Elk Island National Park (Fig. 2.1). All trapping sites were in relatively continuous patches of aspen dominated forest, but these were situated in different surroundings. Sites were categorized as urban, suburban, and rural, based on geographic location and relative isolation from urban activities and structures. Four locations were selected for each site-type or gradient position as described below (see Table 2.1).

Rural sites were characterized by continuous even-aged stands of aspen overstory with mature, well-spaced trees. The terrain varied from rolling hillocks to nearly flat areas. Well-used hiking trails, with only game or livestock trails cutting across them, extended along the trap lines in rural sites. Two rural sites were located in the area of Elk Island National Park, but to ensure that conclusions about rural assemblages did not depend on conditions unique to Elk Island National Park, two sites were also established outside the park. One of those sites (BF) was located in the adjacent Blackfoot Provincial Park and Grazing Reserve. This park is used as

both a cattle pasture and a trail riding area. The trapping site was between the pastures in a large ravine. The other site (BG) was located about 10-15km south of the park, on undeveloped land owned by Dr. Roy T. Berg (Professor Emeritus, and former Dean of the Faculty of Agriculture and Forestry, University of Alberta). The site was cut with extensive cross-country ski trails, but was subject to very little activity from spring to fall.

The suburban or semi-rural sites were located at the periphery of the city of Edmonton. Two sites were located near the edges of the city. One was at a dog walking area near the North Saskatchewan River at the west end of Rabbit Hill Road (RH); the other site was located at the southern end of Edmonton, where 23rd Ave crosses Whitemud Creek (WM). Although only a few small trails extended through the woods where my traps were situated, well used hiking trails were nearby in the surrounding area. Two sites were located further away from the city center: one at the Sherwood Park Natural Area (SH); and one between Edmonton and the city of St. Albert (ST). These 2 sites had terrain similar to that in the rural area. All suburban sites were predominantly flat with only a few steeper inclines.

The urban sites were embedded within the City of Edmonton, but were restricted to ravines and areas in the North Saskatchewan River valley, the only areas in the city with relatively large stands of aspen. The sites were in the Mill Creek Ravine, (ML) near 84th Ave, MacKinnon Ravine (MK) and McKenzie Ravine (MA) near the downtown core and at Laurier Park (LA), in the river valley. Extensive well-maintained walking trails extend through these areas and some areas were actively managed by grass cutting and other activities. McKenzie and MacKinnon Ravines

had no permanent creek bed, but the Mill Creek Ravine included a permanent creek. The urban sites were stands of aspen (*Populus spp.*) more uneven in age with a greater range of tree density than at suburban and rural sites. Urban aspen stands were also more linear and restricted to uneven slopes.

2.2.3 Carabid Assemblages

The study was conducted using standard protocols developed by the Globenet group (Niemelä et al. 2002; see www.helsinki.fi/science/globenet). At each site a single transect of 10 pitfall traps was placed in the straightest line possible through the most continuous forest available. In the urban and suburban sites the traps were placed ~15m apart because of space restrictions, while in the rural sites the traps were about 20-30m apart so as to be consistent with their role in another study in Elk Island National Park. This variation should not have affected the results of the study as pitfall traps in these boreal forest habitats collect statistically independent samples at distances greater than 10 meters apart in this forest type (Digweed et al. 1995). Traps were 1L cylindrical plastic containers with diameters of 10 cm and a depth of 15 cm. Traps were dug in flush to the ground, and each was covered with a small wood roof raised about 3 cm from the ground, as described by Spence and Niemelä (1994).

Traps were filled to a depth of 3 cm with ethylene glycol as a preservative and emptied every 2 weeks. During 1998, the sampling began in the rural areas in the 2nd week of June, and the following week in the urban and suburban sites, and sampling continued until the 4th week in August for a total of 5 sampling periods. In 1999

sampling began in the first week of May and ended in the 4th week of August for a total of 7 sampling periods.

Trap catches were standardized to 50 trapping days in 1998 and 84 trapping days in 1999 and data from both years were pooled by site before analysis. Diversity was calculated using rarefaction (Simberloff 1972), and Simpson's, and Shannon-Wiener indices (Pielou 1975). Both Simpson's and Shannon-Wiener index were used because the former is more sensitive to the dominant species and the latter to rare species (Sit and Taylor, 1998). Evenness of species was calculated using the J function (Pielou 1975). These indices were calculated for the total catch from each of the transects and then compared among site types with ANOVA. Activity-density, taken as a total of the standardized trap catch over both collecting periods, was compared between gradient positions with an ANOVA. Site to site differences were evaluated with Tukey-Kramer post-hoc multiple comparisons.

Similarity of carabid assemblages was depicted using Bray-Curtis percentage similarity, with the unweighted arithmetic average of the season's total catch of each species (standardized) as the clustering measure (Krebs 1989). Two sets of analyses were completed using data from both years; one including both introduced and native species and the other only the native fauna. The 2 sets were then compared to give a clearer understanding of the impact of introduced species on the carabid assemblages.

2.2.4 Wing Length

Wing length was recorded for each specimen of *Agonum retractum* Leconte (a wing dimorphic native species), and *Pterostichus melanarius* Illiger (a wing dimorphic introduced species) in 1998, either as "long" for macropterous individuals

with wings that were fully extended and reflexed at the tip when folded or "short" in brachypterous individuals with wings reduced to sizes that cannot function in flight (Lindroth 1961-69, Carter 1976). Wing morph frequencies were calculated for each transect and compared with two-way ANOVA using species, and gradient position as factors in 1998. In 1999, only *P. melanarius* wing lengths were recorded, but data were tallied separately for males and females to establish if sex affected wing dimorphism. The two-way ANOVA used gradient position and sex as factors in analysis of data from 1999. The data were also subjected to chi-square tests to determine if the sites within an area type (urban, suburban, or rural) were homogeneous for wing morph frequencies.

2.2.5 Disturbance Measures

Anthropogenic disturbance was quantified at two scales relevant, respectively, to landscape and site considerations. The landscape approach used a satellite photo to assess: 1) the percentage green space in a approximately 1 km^2 area centered on the site; and 2) the distance to the city center as measured from the center of the downtown core. At the site level, 3 characteristics were measured: 1) soil bulk density at three locations on secondary paths, in the forest, and on primary paths; 2) secondary path density; and 3) density of discarded trash.

Soil compaction, which should be in proportion to human use of walking paths, was assessed as a measure of human activity. Soil bulk density was measured in samples taken using a soil corer 9 cm deep x 4 cm in diameter. Each core was divided into three equal volumes (top, middle and bottom) and final weights of these volumes of soil were determined after drying. At each site, soil cores were taken

from three secondary small paths and three places in the forest, along the pitfall transect spaced approximately 25m apart. One core was taken from a primary path to assess the amount of foot traffic.

Path density was estimated by counting path intercepts along four 25m transects perpendicular to the main transect. Counting the number of trash items (trash density) apparent along these same four transects 1 m on either side of the transect provided another estimate of human activity.

Simple linear regression was used to seek relationships among the Shannon-Wiener diversity measure (including introduced species) and activity density (including introduced species) and the measures of disturbance. (For soil bulk densities only data from the top 3cm are presented as they gave the strongest regressions and showed the greatest variance in soil compaction. In areas where the soil was too dense to allow a soil core to be taken, cores were arbitrarily assigned a weight of 600g (200g for each third of the core), which was greater than all other core samples.)

2.3 RESULTS

2.3.1 Carabid Assemblages and the Gradient

The several measures of species diversity showed similar patterns. Rarefaction estimates of species diversity showed a significant pattern of decreasing diversity with increasing urbanization ($F = 10.4$, $df = 2, 7$, $P = 0.008$; Fig. 2.2). Values for the Shannon-Wiener index were significantly higher at the rural end of the gradient ($F = 12.0$, $df = 2, 7$, $P = 0.005$; Fig. 2.3). Simpson's index or dominance showed similar patterns ($F = 9.0$, $df = 2, 7$, $P = 0.012$; Fig. 2.4). The J function, (Fig.

2.5) showing decreasing evenness, was associated with increasing urbanization ($F = 9.6$, $df = 2, 7$, $P = 0.010$).

The basis of differences along the gradient was illuminated by excluding the introduced species from the analysis. Without introduced species, the pattern of decreasing diversity with increasing urbanization was no longer significant for any of the measures mentioned above (Rarefaction: $P = 0.102$, Fig. 2.2; Shannon-Wiener: $P = 0.183$, Fig. 2.3; Simpson's: $P = 0.270$, Fig. 2.4; J function: $P = 0.513$, Fig. 2.5).

The mean activity-density of carabid beetles captured per site (Fig. 2.6) was > 8 times higher at the urban end of the gradient ($P = 0.085$), but differences were statistically insignificant given the large intersite variation. Neither were these differences significant ($P = 0.605$) between sites without the introduced species included (Fig. 2.6), even though about twice as many carabids were captured in urban as opposed to rural sites. In fact, three introduced species (*Carabus nemoralis* Müller, *Carabus granulatus* Linne, and *Pterostichus melanarius* Illiger, Fig. 2.7) dominated in the urban and suburban areas, accounting for 84.8% of the total catch in urban sites and 49.3% in suburban sites. In contrast, introduced species constituted a minor and highly variable proportion (1.4%) of the total rural catch. Interestingly, the proportion of native fauna (Fig. 2.8) that represents rare and uncommon species (less than 5% total native catch in all gradient positions) was greater in rural (18.7%) and suburban areas (17.6%) than in urban areas (9.7%).

In an ordination analysis of Bray-Curtis similarity values including the introduced species, the replicates at each gradient position clustered more or less together (Fig. 2.9). However, with only native species in the ordination, the sites did

not cluster particularly well, suggesting that the introduced species were responsible for most of the assemblage structure observed in the response to the gradient.

2.3.2 Introduced Species and the Expansion of *P. melanarius*

Four introduced species, with origins in Western Europe, reached their maximum abundance in the urban sites. *Carabus granulatus, Carabus nemoralis,* and *Clivina fossor* Linne were found exclusively in the urban and suburban areas. *Pterostichus melanarius* was found in all areas and was also the most abundant introduced species throughout the gradient. In fact, *P. melanarius* was the most common of carabid species in both the urban and suburban areas. During a study in Elk Island National Park in 1998 (E.D. Montes de Oca, D.J. Hartley, and J.R. Spence, unpublished), captures of *P. melanarius* were only slightly less than for *Calathus ingratus* Dejean, which was the most common rural species. In the present study, however, using sites outside the park, *P. melanarius* was less abundant in rural areas than native species like *Platynus decentis* Say and *C. ingratus* (Fig. 2.8).

Patterns of wing dimorphism (Fig. 2.10) differed significantly between the native *A. retractum* and introduced *P. melanarius*. No effect of the gradient was noted on proportion of macropterous (long-winged) individuals for *A. retractum*, populations of which had a mean of 11.5% +/- 3.7 macropterous individuals. In contrast, *Pterostichus melanarius* showed a significant increase in macroptery at the rural end of the gradient in data from both 1998 ($F = 18.6$, $df = 5,18$, $P < 0.001$) and 1999 ($F = 66.8$, $df = 5, 14$, $P < 0.001$). In 1999, significant effects were also noted for sex ($P < 0.001$), and the interaction term between sex and gradient position ($P < 0.001$) (Fig. 2.11). The pattern in both males and females was that of decreasing

macroptery with increasing urbanization. However, females showed a greater incidence of macroptery toward the rural end of the gradient.

2.3.3 Landscape and Stand Features Associated with Carabids

Site-level measures of disturbance were poor predictors of carabid activity-density. Only bulk soil density of primary paths was significantly related to carabid activity-density ($F = 11.8$, $df = 1, 8$, $P = 0.009$; Fig. 2.12a). None of the other factors measured were significant predictors of carabid activity-density ($P = 0.544 – 0.896$). Contrary to expectations, areas with more soil compaction along primary paths had higher activity-density.

Regressions of carabid diversity on site-level disturbance were insignificant. Decreases in soil bulk density along primary paths ($F = 4.9$, $df = 1, 8$, $P = 0.057$; Fig. 2.12b) were marginally associated with increases in carabid diversity. Interestingly, soil bulk density in the forest and along secondary paths, path density, and amount of discarded material along the transects were not strong predictors of carabid species diversity ($P = 0.086 – 0.995$).

Percent green cover was a significant predictor of carabid activity-density. As % green cover in the landscape increased carabid activity density decreased ($F = 7.1$, $df = 1, 8$, $P = 0.029$; Fig. 2.13a). Carabid activity density also decreased as distance from the city center ($F = 4.9$, $df = 1, 8$, $P = 0.058$; Fig. 2.14a) increased, although it was marginally insignificant.

At the landscape level, % green cover and distance from city center were both significant predictors of carabid diversity. As % green cover in the landscape ($F = 12.6$, $df = 1, 8$, $P = 0.008$; Fig. 2.13b) increased, carabid diversity increased. Carabid

diversity also increased as distance from the city center ($F = 5.3$, $df = 1, 8$, $P = 0.050$; Fig. 2.14b) increased.

2.4 DISCUSSION

I address three main points in this discussion. The first is how the urban-rural gradient affects carabid assemblages, specifically the effects of urbanization on carabid assemblages. The second topic is an analysis of the expansion of *P. melanarius*. *Pterostichus melanarius* is the only introduced species found in all gradient positions, and it may affect the native carabid fauna if its expansion continues. The third point is how landscape and stand features are associated with patterns of carabid diversity and activity-density.

2.4.1 Carabid Assemblages and the Urban-Rural Gradient

Carabid assemblages could be affected by two possible factors studied here: 1) the urban-rural gradient, and 2) the presence of introduced species and their response to the gradient. Decreases in carabid diversity in urban areas have been attributed directly to the gradient (Davis, 1978). In the present study, it is not possible to distinguish between the effects of urbanization on diversity versus the effects of introduced species on the native assemblage. Significant patterns in estimated species numbers or diversity indices were not observed, but uncommon or rare native species comprise a larger percentage of the total assemblage as urbanization decreases (Fig. 2.8). These results appear to be consistent with those of a previous study in Edmonton by Niemelä and Spence (1991) who reported no significant difference or pattern between rural and urban diversity (as measured by H'). However, overall my findings (marginally insignificant patterns and overall

trends in the data) concur with results from Helsinki, Finland (Niemelä et al. 2002), where carabid diversity decreased with increased urbanization. In summary, it seems that the urban environment may have an effect on the overall structure of the community assemblage, similar to that suggested in urban areas for British Columbia (Spence and Spence 1988). In western Canada this effect depends largely on the presence of introduced species.

The specific factors that cause diversity to fall in urban areas have not been determined. I believe that a combination of habitat structural changes and associated microclimatic effects in the urbanized habitat could diminish survival and/or reproduction of some carabids even though overall activity density is higher. In addition, simplification of habitat may have eliminated pockets of special habitat required by particular rare species (Davis 1978). In Europe, habitat fragmentation is thought be associated with local extirpation of populations of some carabid species (De Vries and Den Boer 1990). It may also be that this drop in rare species reflects long-term competition with introduced carabids (Spence and Spence 1988), but this is not apparent in data about relative abundance presented here.

Although activity density of carabids is highest in urban areas, long-term data suggest that changes in abundance favour the introduced species. In earlier studies carried out in the Edmonton area, Niemelä and Spence (1991, 1994) reported a 3-fold greater activity density of native carabids in urban than in similar rural sites, but no significant difference could be demonstrated across the gradient in data for 1998-99. However, activity densities of native species have decreased markedly with the increase in activity density of *P. melanarius, C. nemoralis*, and *C. granulatus* in 8

years since the Niemelä and Spence (1991) study. This suggests possible increases in competition with the passage of time. Such interactions could not be demonstrated clearly in a field experiment conducted in the aspen forest (Niemelä et al. 1997); however, in that field experiment densities of *P. melanarius* were likely lower than those in Edmonton today, and neither *C. nemoralis* nor *C. granulatus* were included.

Carabids are generalist predators and are usually restricted in size of prey by only their own size (Wheater 1988). Interference competition has been demonstrated between *P. melanarius* and *Pterostichus adstrictus* Eschscholtz in laboratory experiments (Currie et al. 1996). The relative drop in native activity density from the 1990 study, and the rise in activity density and numbers of introduced species captured in this study suggest that interference competition could be acting presently in the Edmonton area. Also, in the early 1990's, local assemblages in Edmonton were dominated by *P. adstrictus* (Niemelä and Spence 1991), although this species is now only a modestly abundant component of the native community. Both *C. nemoralis* and *C. granulatus* are large bodied carabids, and the individuals of these species could easily prey on native species, most of the latter being medium to small in size.

The idea that urbanization favours introduced species disproportionately is further supported by the ordination analysis, which shows clear separation of site types only with introduced species included. The differences in assemblages were due entirely to the presence of introduced species and their interaction with the gradient. No clear effect of the gradient on native assemblages was found in the

ordination; thus native assemblages appear similar in urban areas to those in rural areas.

For introduced species several trends are evident. In 1990, *P. melanarius* was the only introduced species that represented a major component of the urban assemblage in Edmonton (Niemelä and Spence 1991, 1994), and it was present at a much lower proportion (17%) of the total activity density. In contrast, *P. melanarius* accounted for 70.5% of the urban ground beetle activity density during 1998 and 1999. In addition, two other introduced species [*C. nemoralis* (6.4%) and *C. granulatus* (7.9%)] both present at lower activity densities in previous studies, now make up a significant proportion of the urban fauna. Thus, over the past 8 years, these 3 introduced species appear to have become better established and more successful in urban Edmonton. It is unclear whether the two *Carabus* species will become as common as *P. melanarius*. The lower vagility of both *Carabus* species may exclude them from the rural forests (*C. nemoralis* and North American populations of *C. granulatus* are brachypterous (Lindroth 1961-69, pp.38 and 37) or it may simply be a matter of time before they get there.

Species introduced from Europe may have several advantages over the native fauna in North American urban areas. Anthropogenic habitats, including urban environments have been common in Europe for a longer time than in North America, perhaps allowing for a greater biotic adjustment to urban conditions (Spence 1990). These introduced species living in Edmonton are common in urban or disturbed habitats in Europe (Thiele 1977) but there they do not dominate as they do here (Spence 1990). This suggests either that controls on populations in Europe may be

absent from North America or that in North American urban areas competition from other species adapted to urban environments is lacking.

2.4.2 Expansion of *Pterostichus melanarius*

Niemelä and Spence (1991) reported that *P. melanarius* was more abundant in urban sites, but that the proportion of macropterous individuals in rural areas was greater.

Patterns of wing dimorphism suggest that *P. melanarius* is expanding its range away from Edmonton by flight, as found in a previous study (Niemelä and Spence 1999). In *P. melanarius*, the brachypterous (short wing) form behaves as a simple Mendelian dominant trait and the macropterous (long wing) form is recessive (Aukema et al. 1996). Therefore, a local population dominated by macropterous individuals is mostly made of dispersing migrants from other sources. The occurrence of macropterous individuals in urban areas has decreased from 20% (Niemelä and Spence 1991) to less than 5% (6% in 1999) while the proportion of macropterous individuals continues to remain high in rural areas. Macroptery appears to be more frequent among females than males along the gradient. If a predominance by brachypterous individuals is an indicator of spatially stable population (Den Boer 1970), then the population of *P. melanarius* has become much more stable over the last 8 years in the urban environment of Edmonton. In fact, rates of brachyptery are almost at the levels characteristic of established European populations (~98%) (Den Boer and Van Dijk 1996).

What is occurring at the rural end of the gradient remains unclear. Rural populations of *P. melanarius* are still being established in areas outside of the city,

with road verges and other areas acting as corridors for colonization of the rural habitat (Niemelä and Spence 1991, 1999). A prior study suggests that *P. melanarius* is capable of establishing populations in aspen forests (Niëmela et al. 1997) and it is likely that this species will spread farther and establish spatially stable (predominantly brachypterous) populations well beyond the urban center.

2.4.3 Landscape and Stand Features Associated with Carabids

The diversity of the carabid assemblage decreased and activity density increased with increasing soil density on primary paths. People on day outings tend to remain on the main paths and the large number of people using these urban forests probably leads to a greater compaction of soil. Why the extent of local human activity should be associated with increased activity density of carabids is not known. The trend toward lower carabid diversity with increasing soil bulk density, together with the results about activity density of carabids, suggests that local human activity favours the introduced species.

Two patterns emerged from the measurements of disturbance at the landscape level for both diversity and activity density. As the amount of green cover increased around the sites, carabid diversity increased, and activity density decreased. The urban habitat is more fragmented and made up of patches of forest surrounded by urban development, and fragmentation, at this scale, appears to affect some carabid populations negatively (De Vries and Den Boer 1990). However, fragmentation associated with urban habitats may favour species characteristic of habitat edges like these introduced species (Spence 1990). Proximity to the city center was also associated with lower carabid diversity and increased activity density. Habitats near

the city center are apparently less suitable for rare species, possibly reflecting the loss of microhabitats on which such species depend (Davis 1978).

In general, measures of disturbance at the landscape level explained patterns of carabid diversity better than did disturbance measures at the site level. This suggests that small-scale management of greenspace quality is not as important for maintenance of carabid diversity as is management at the landscape level. Landscape measures had lower R^2 values than site level measures of disturbance for explaining activity density. Thus, management at the site level would be more important for promoting features that affect the size of natural carabid populations.

2.4.4 Conclusions

This study illustrates the effect of urbanization on introduced carabid species locally. Some weak evidence indicates that urbanization has a negative effect on rare species, and stronger evidence indicates that introduced carabids are positively affected by urbanization. Results from this study suggest ways of protecting the biological integrity of urban forests. A landscape perspective suggests that greenspaces should be set aside and that they must be large enough to maintain the range of habitats required to support the full range of native species diversity.

Table 2.1. List of Aspen Forest Sites. Classification, names and designation of sites where pitfall traps were installed on Edmonton-Elk Island National Park urban-rural gradient.

Gradient Position	Site Name	Abbreviation
Urban	Mill Creek Ravine	ML
	MacKinnon Ravine	MK
	McKenzie Ravine	MA
	Laurier Park	LA
Suburban	Rabbit Hill Road	RH
	Whitemud Creek Ravine	WM
	St. Albert	ST
	Sherwood Park Natural Area	SH
Rural	Elk Island National Park-1	M-1
	Elk Island National Park-2	M-2
	Blackfoot Provincial Park	BF
	Dr. Roy Berg's land	BG

Table 2.2. Species List of Aspen Forest Carabid Assemblages. Classification of rare versus common species, and gradient positions found at, across the Edmonton-Elk Island National Park urban-rural gradient. (U = urban, S = suburban, R = rural), (* = introduced species)

Species Name	Status	Gradient Position
Pterostichus adstrictus Eschsholtz	Common	U, S, R
P. pensylvanicus Leconte	Common	U, S, R
Calathus ingratus Dejean	Common	U, S, R
Synuchus impunctatus Say	Common	U, S, R
Agonum sordens Kirby	Common	U, S, R
A. retractum Leconte	Common	U, S, R
Platynus decentis Say	Common	U, S, R
Pterostichus riparius Dejean	Common	U, S
Loricera pilicornis Fabricius	Rare	U, S, R
Patrobus foveocollis Eschscholtz	Rare	U, S, R
Trechus apicalis Motschulsky *Agonum gratiosum* Mannerheim	Rare	U, S, R
	Rare	U, S, R
A. corvus Leconte	Rare	U, S, R
A. placidium Say	Rare	U, S, R
Harpalus fulvilabris Mannerheim	Rare	U, S, R
Bradycellus lugubris Leconte	Rare	U, S, R
Chlaenius alternatus Horn	Rare	U, S, R
Cymindis cribricollis Dejean	Rare	U, S, R
Nebria gyllenhali Schönherr	Rare	U, S
Poecilus lucublandus Say	Rare	U, S
Agonum piceolum Leconte	Rare	U, S
A. cupreum Dejean	Rare	U, S
Amara cupreolata Putzeys	Rare	U, S
Carabus chamissonis Fischer	Rare	S, R
Calosoma frigidum Kirby	Rare	S, R
Patrobus stygicus Chaudior	Rare	S, R
P. septentrionis Dejean	Rare	S, R
Bembidion fortestriatum Motschulsky	Rare	S, R
Agonum thoreyi Dejean	Rare	S, R
Platynus mannerheimi Dejean	Rare	S, R
Amara quenseli Schönherr	Rare	U
Scaphinotus marginatus Fischer	Rare	S
Harpalus ventralis Leconte	Rare	S
Patrobus lecontei Chaudoir	Rare	R
Agonum superioris Lindroth	Rare	R
A. propinquum Gemminger & Harold	Rare	R
Amara hyperborea Dejean	Rare	R
Pterostichus melanarius Illiger*	N/A	U, S, R
Carabus granulatus Linné*	N/A	U, S
C. nemoralis Müller*	N/A	U, S
Clivina fossor Linné*	N/A	U, S

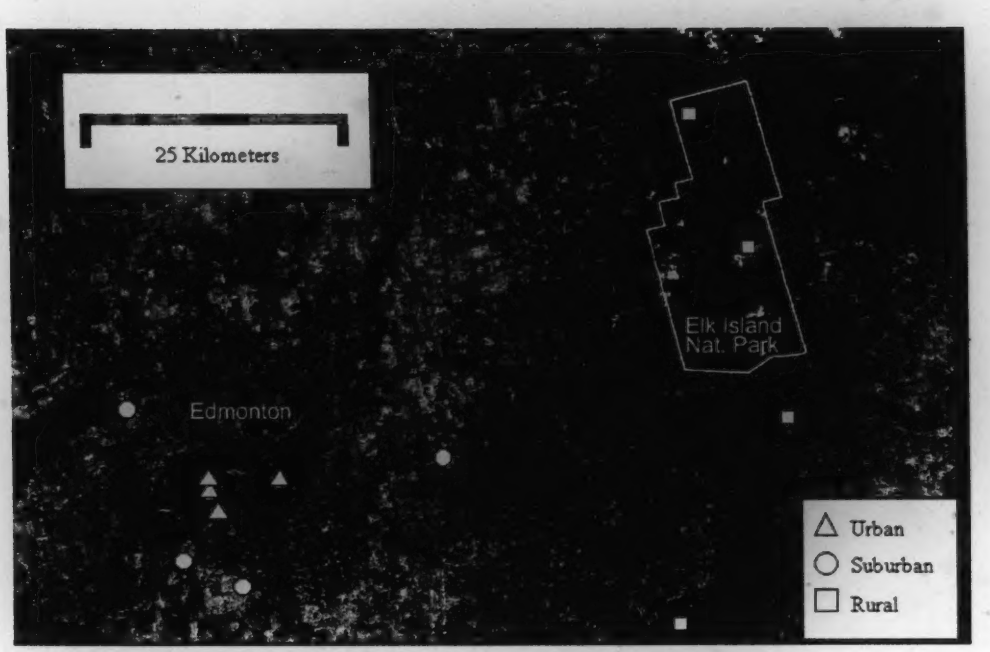


Fig. 2.1. Satellite Image of the Aspen Urban-Rural Gradient. The locations of the study sites by gradient position is shown

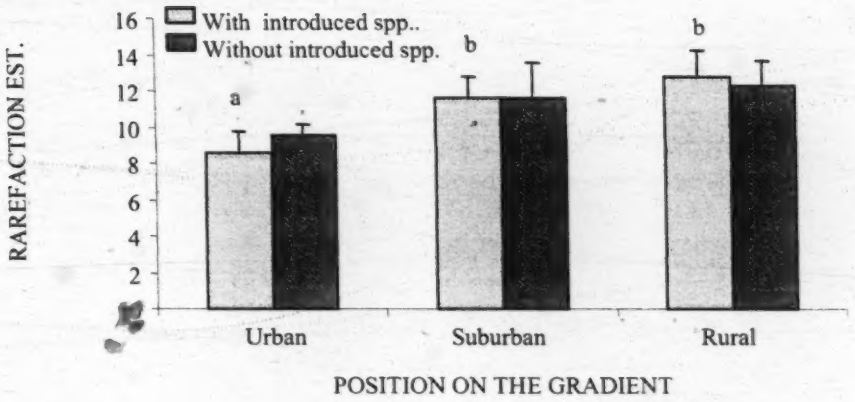


Fig. 2.2. Rarefaction Estimates of Diversity Along Aspen Gradient. Rarefaction estimate of species diversity per site along the urban-rural gradient for a sample of 100 individuals for 1998 and 1999 both with and without introduced species included in the analysis. Standard error bars and letters representing Tukey-Kramer multiple comparisons included.

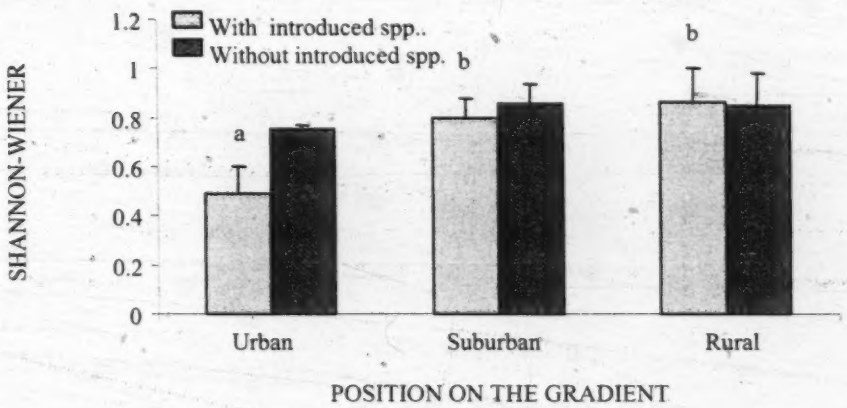


Fig. 2.3. Shannon-Wiener Estimates of Diversity Along Aspen Gradient. Shannon-Wiener index along the urban-rural gradient for 1998 and 1999 with and without introduced species included in the analysis. Standard error bars and letters representing Tukey-Kramer multiple comparisons included.

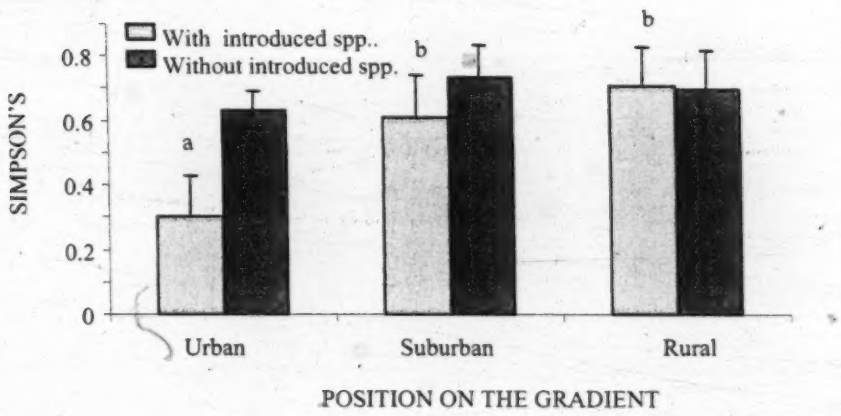


Fig. 2.4. Simpson's Estimates of Diversity Along Aspen Gradient. Simpson's index along the urban-rural gradient for 1998 and 1999 with and without introduced species included in the analysis. Standard error bars and letters representing Tukey-Kramer multiple comparisons are included.

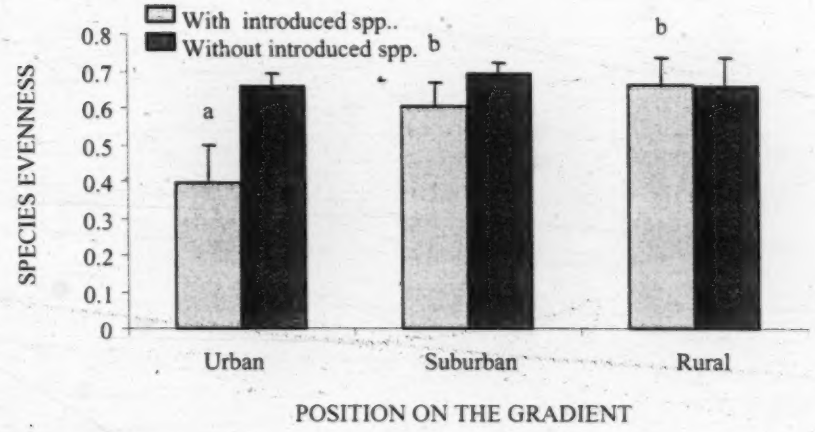


Fig. 2.5. Species Evenness Along Aspen Gradient. J function along the urban-rural gradient for 1998 and 1999 with and without introduced species in the analysis. Standard error bars and letters representing Tukey-Kramer multiple comparisons included.

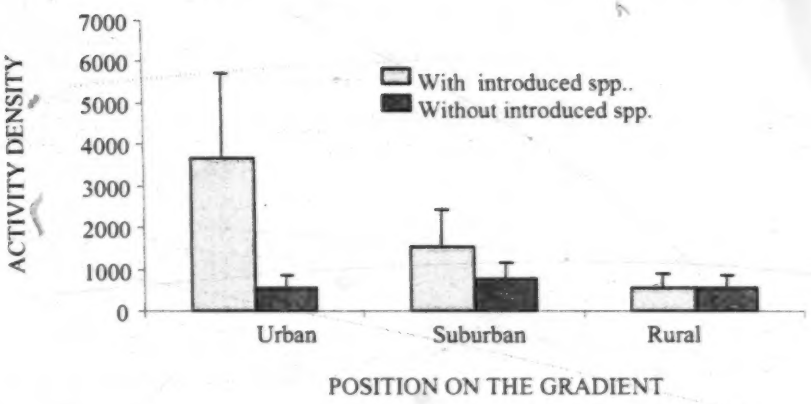


Fig. 2.6. Total Activity-Density Along Aspen Gradient. Mean standardized activity density along the urban-rural gradient in 1998 and 1999 with and without introduced species in the analysis. Standard error bars included.

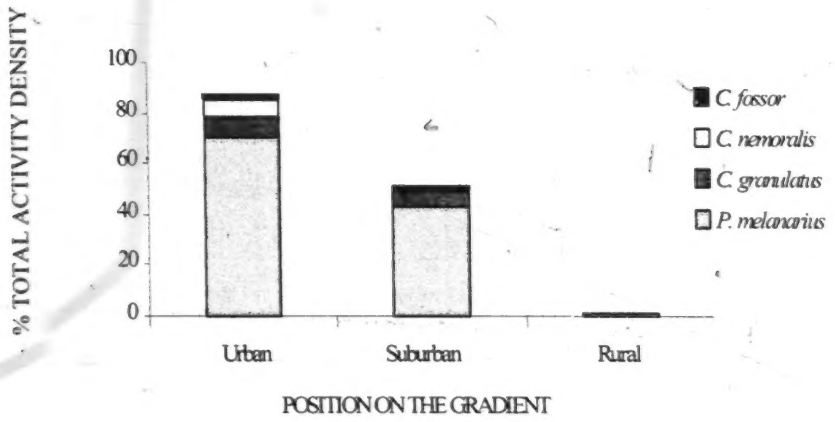


Fig. 2.7. Introduced Species Activity-Density Along Aspen Gradient. Introduced species activity density as a percent of standardized season total along the urban-rural gradient for 1998 and 1999.

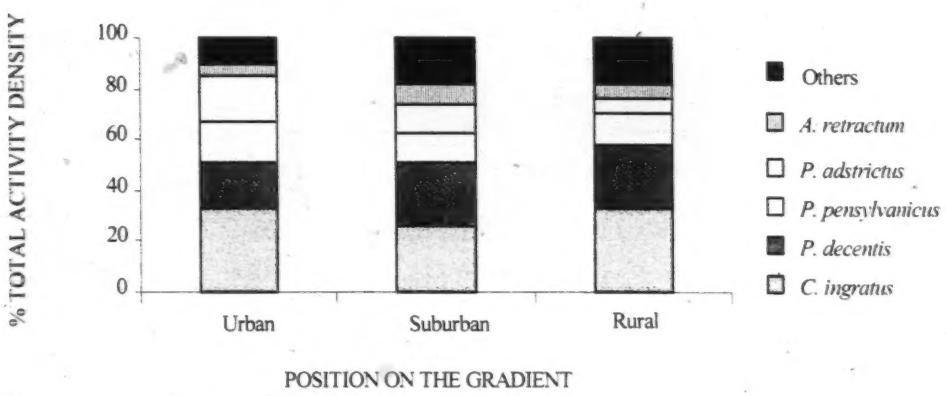
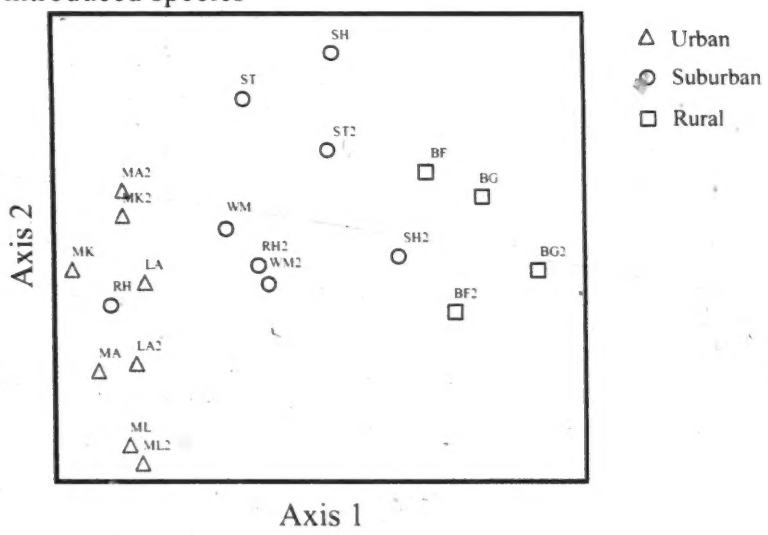


Fig. 2.8. Native Species Activity-Density Along Aspen Gradient. Native species abundance as percent of standardized season total of native species only along the urban-rural gradient for 1998 and 1999.

a) with introduced species



b)without introduced species

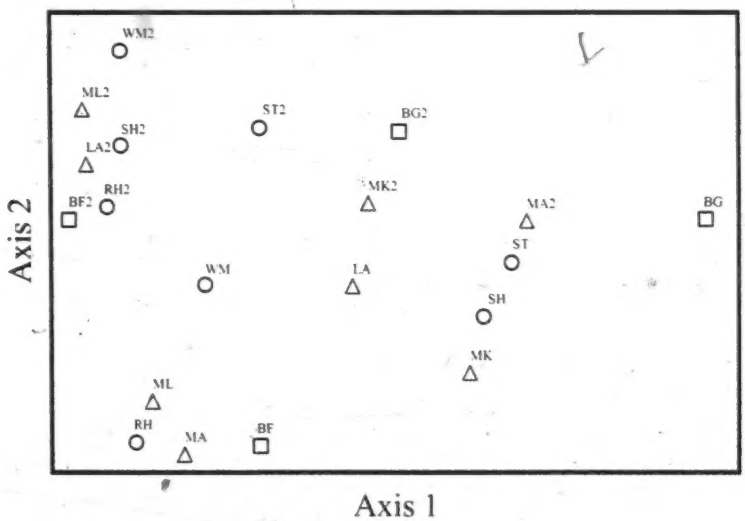


Fig. 2.9. Bray-Curtis Ordination of Sites Along Aspen Gradient. Bray-Curtis ordination plots along the urban-rural gradient for 1998 and 1999 for a) the entire assemblage and b) native species only

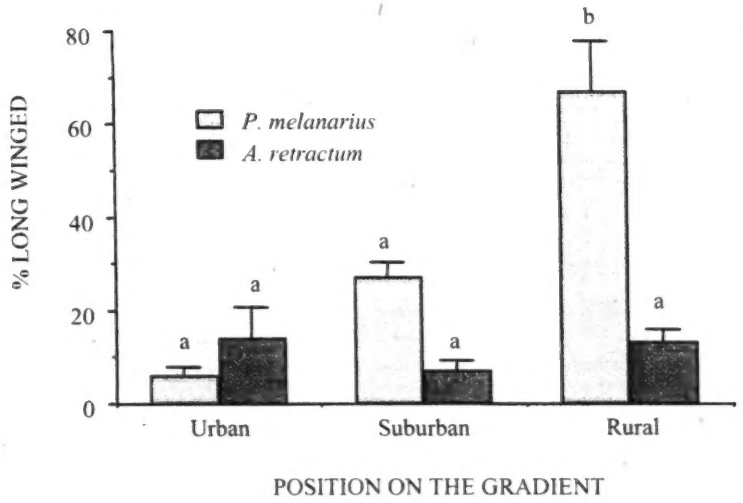


Fig. 2.10. Wing Dimorphism Along Aspen Gradient in 1998. Wing dimorphism (% long winged individuals in population) in *Pterostichus melanarius* (introduced) and *Agonum* retractum (native) along the urban-rural gradient. Standard error bars and letters representing Tukey-Kramer multiple comparisons included.

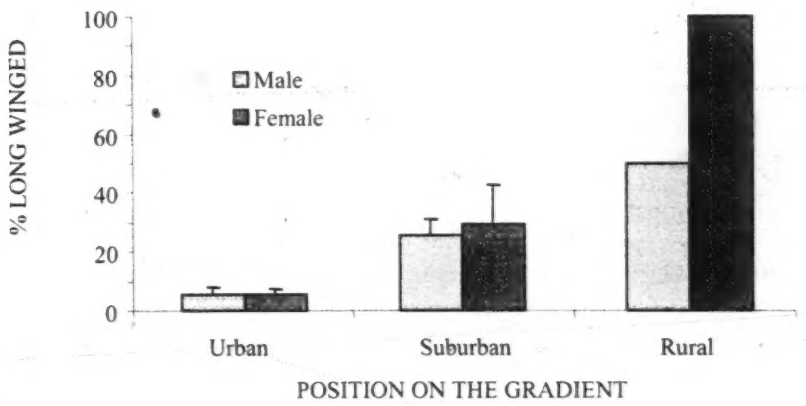


Fig. 2.11. Wing Dimorphism Along Aspen Gradient in 1999. Male and female *Pterostichus melanarius* wing dimorphism (% of long winged individuals in population) over the urban-rural gradient. Standard error bars included, but in rural sites are too small to see.

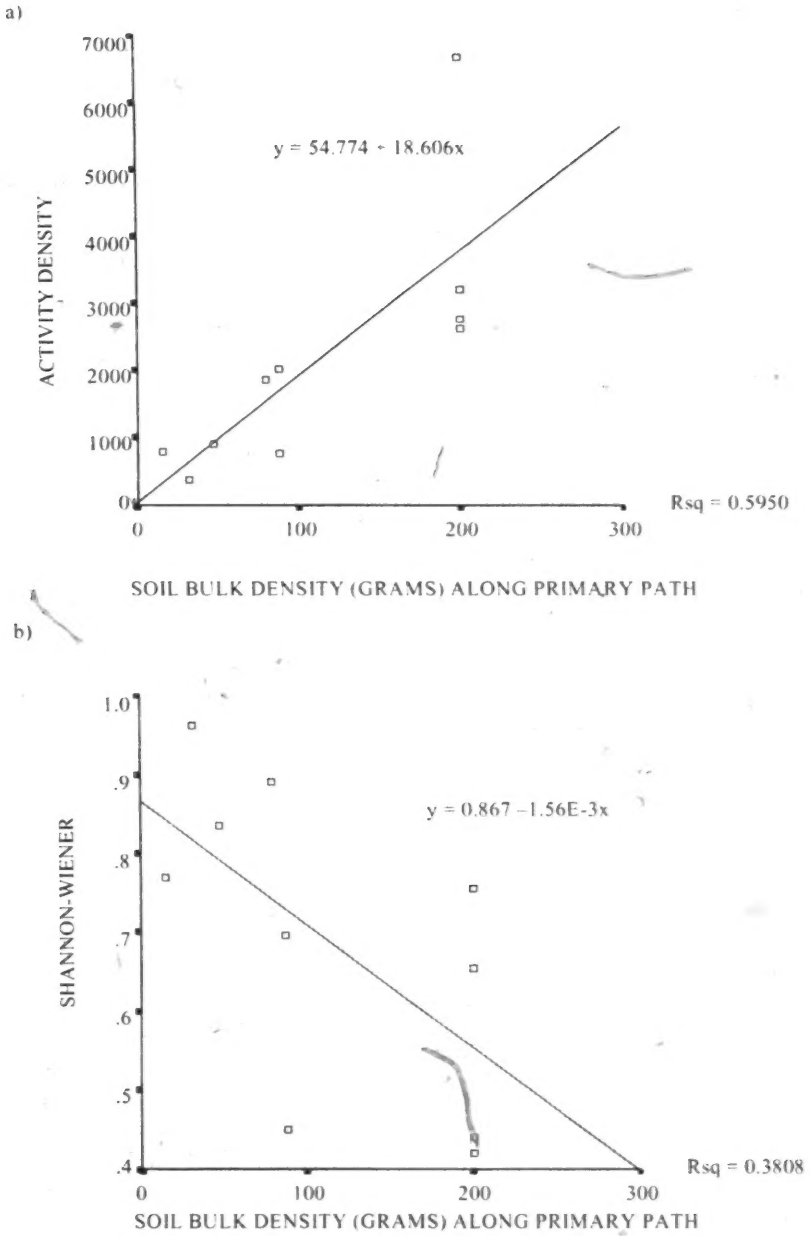


Fig. 2.12. Relationships of Soil Bulk Density Along Aspen Gradient. Linear regression for the soil bulk density of the top 3cm of soil on the primary path versus a) activity density and b) Shannon-Wiener index including introduced species in the analysis.

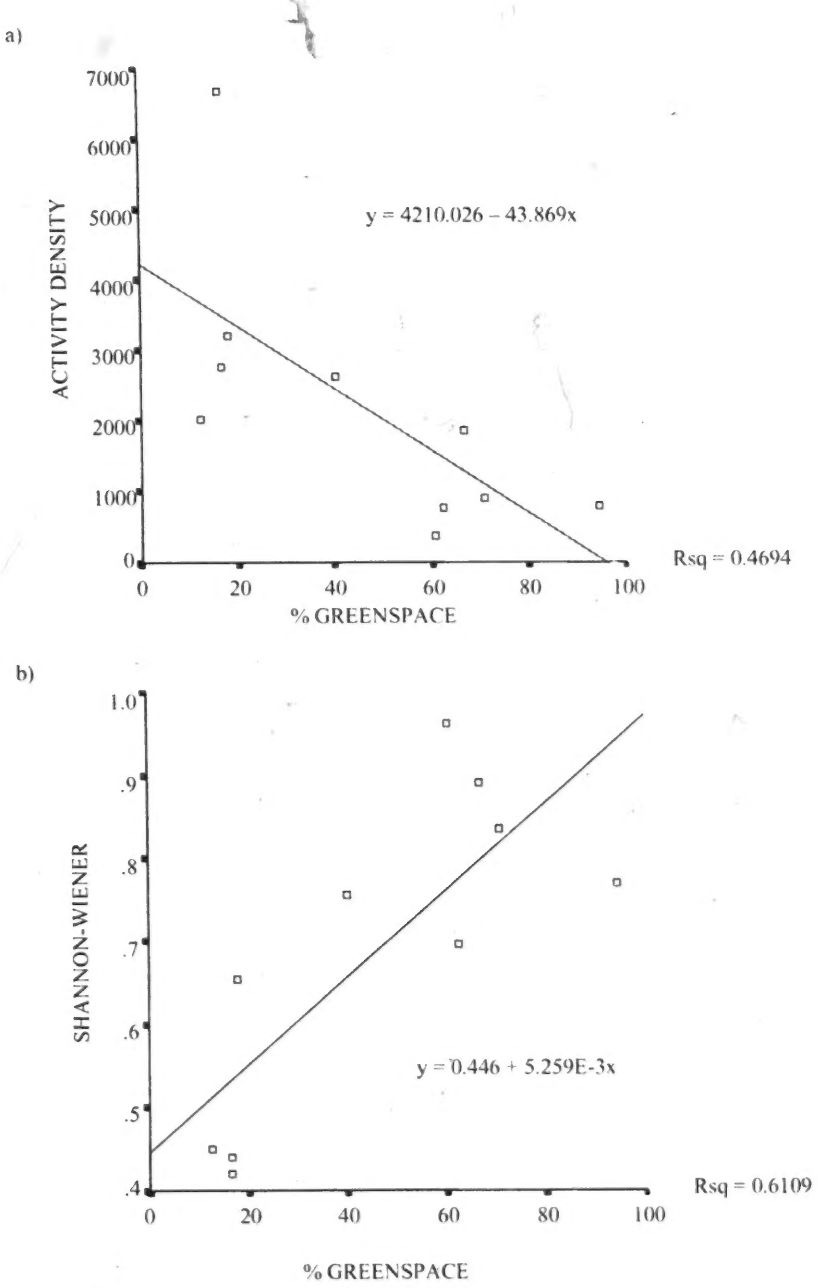


Fig. 2.13. Relationships of % Green Cover Along Aspen Gradient. Linear regression of % green cover in area surrounding sites along the urban-rural gradient versus a) activity density and b) Shannon-Wiener Index including introduced species.

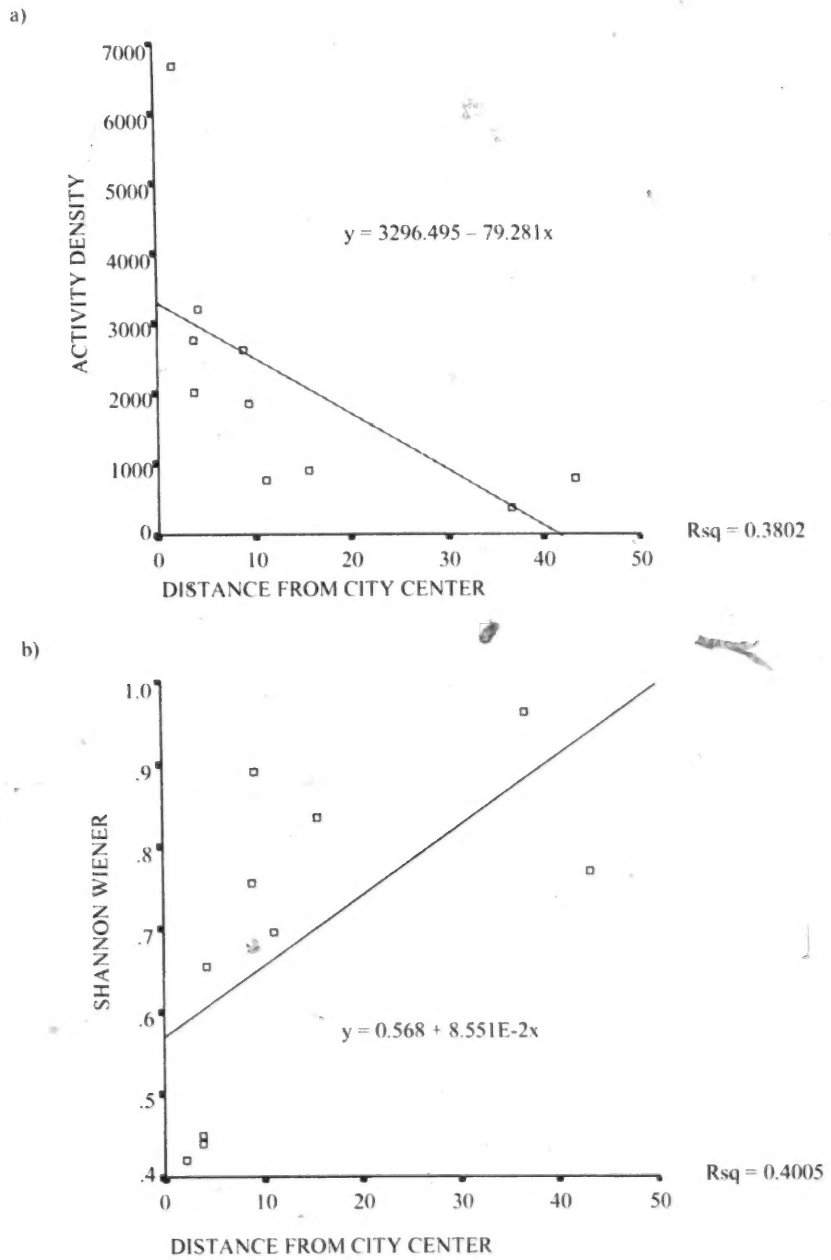


Fig. 2.14. Relationships of Distance From City Center Along Aspen Gradient. Linear regression of distance from the city center along the urban-rural gradient versus the a) activity density and b) Shannon-Wiener index including introduced species.

CHAPTER THREE

THE EFFECTS OF LANDSCAPE AND GRASSLAND HABITAT QUALITY ON CARABID BEETLES ALONG AN URBAN-RURAL GRADIENT

3.1 INTRODUCTION

Urbanization leads to alteration of both the landscape (general disturbance regime, air pollution, climate and broad hydrological effects) and habitat quality for the biota (e.g., plant communities, amount and distribution of litter, direct physical changes, and local hydrological aspects) (McDonnell and Pickett 1990, Pickett et al. 2001). In addition to selective pressures from these effects, urban environments place native species in regular contact with introduced taxa (e.g., Airola and Buchholz 1984, Niemelä and Spence 1991). Urbanization is commonly linked with negative impacts on native taxa (McDonnell and Pickett 1990).

Recent trends in ecosystem assessment involve defining bio-indicator groups (supra-generic taxa of familial to class rank) composed of species sensitive to changes in the local environment that provide measurable responses to changes in the system (Dufrêne and Legendre 1997, Desender et al. 1997, Luff 1996, Stork 1990). A currently accepted method for ecosystem study involves a complementary approach toward defining human impacts in landscape ecology, using landscape gradients to assess effects of complex changes in urbanization (Ter Braak and Prentice 1988). The gradient paradigm postulates that environmental variation is ordered in space and that resulting habitat modifications affect the structure and functional relations of the organisms in that space (McDonnell and Pickett 1990). By measuring differences along the gradient in the community structure of the chosen bio-indicator group, the

paradigm holds that changes associated with increasing intensity of the gradient type may be discovered. The analytical utility of the paradigm depends on the assumption that, prior to the disturbance (e.g., urbanization), assemblages of the indicator taxon were more or less uniformly structured along the gradient.

I set out to study what aspects of a northern assemblage of carabid beetles result from the effect of the landscape pattern associated with urbanization and which aspects more properly reflect variation in habitat quality. Knowing which biotic effects of urbanization are due to changes in landscape patterns and which are due to changes in habitat quality may guide development of approaches to management of urban biodiversity.

As a bioindicator group, I chose the ground beetle family Carabidae because it is diverse, with generally abundant species and individuals that are sensitive to habitat variation, well known taxonomically, and easy to collect (Spence et al. 1996). In the Holarctic Region, carabids are primarily litter-dwelling predators of macro-invertebrates (Lindroth 1969, p.XXXIII). The habitats studied across the urban-rural gradient were open habitats referred to here as "grasslands" and "graveyards". In this chapter I aimed to meet the following three main objectives.

1) Determine by comparison if the carabid assemblages of grasslands and graveyards are distinct, and if so, to identify habitat characteristics that could promote such differences.

2) Identify gradient effects in the two habitat types. I expected that urban and suburban habitats should have assemblages more similar to those in earlier successional stage or highly disturbed habitats than those found in rural sites

(Strueve-Kusenberg 1980), reflecting change in response to the degree of urbanization.

3) Partition the effects of landscape patterns and habitat quality on carabid assemblages between landscape and more local, habitat-dependent effects. I predicted that gradient patterns in graveyard carabid assemblages would reflect mainly landscape effects because these habitats are so homogeneous (and ecologically monotonous). Grassland assemblages, in contrast, should show more variation in carabid assemblages because of habitat variation and reflect both landscape and habitat effects.

3.2 MATERIALS AND METHODS

3.2.1 Materials

The study material obtained by pitfall trapping comprised a total of 3163 adult carabid specimens representing 22 species. Carabid adults were identified to species using the keys and descriptions provided by Lindroth (1961-69). However, generic names and specific epithets follow Bousquet and Larochelle (1993). Specimens were either pinned or stored in 70% ethanol. Voucher specimens were deposited in the E. H. Strickland Entomological Museum of the Department of Biological Sciences, University of Alberta.

3.2.2 Study Sites

Ground beetles were trapped during the summer of 2000 along a landscape gradient extending from Edmonton, Alberta eastward 60 km past Elk Island National Park (EINP) (Fig. 3.1). All sites were situated in patches of grassland or in graveyards. Sites were categorized as urban, suburban, and rural, based on geographic location and their relative isolation from urban activities and structures.

Each combination of habitat and gradient position was represented by four locations, for a total of 24 sites. Grasslands and graveyards differed conspicuously in vegetation cover. Graveyards were regularly mowed and occasional woody plants were interspersed throughout the habitat along with the headstones. All grassland sites, in contrast, were unmowed, supported dense, tall, grassy vegetation by mid summer, and had fewer woody plants.

Rural sites were located at least 45 km east of Edmonton and were surrounded completely by agricultural land or forest. Rural graveyards were considerably smaller than their urban counterparts. However, the rural grasslands were similar in size to those in urban areas. Rural sites saw relatively little traffic from humans or wildlife, as indicated by direct sighting, pathways and other signs. Both types of rural habitats were small (approx. 0.2-0.5 ha) patches, isolated from patches of similar habitat.

The suburban sites (Table 3.1) were located on the periphery of the city and were surrounded by urban sprawl or agricultural land. Human traffic in suburban sites was more frequent than in rural sites, but less than in urban sites. Suburban grasslands were the largest sites (1-3 hectares) in this study, but suburban graveyards were more variable in size, spanning the entire range observed for graveyards in this study (0.2-3 hectares).

The urban sites (Table 3.1) were located within 5 km of the city center and were bounded by urban development or by the North Saskatchewan River valley. Human traffic at these sites was frequent and substantial. Urban graveyards were at the upper end of the size range observed for graveyard sites (3 hectares), and had more ornamental trees scattered throughout than either suburban or rural sites. Urban

grasslands were isolated undeveloped patches as small as the rural grasslands (0.2-0.5 hectares).

3.2.3 Sampling methods

At each site a 3 x 2 grid of 6 pitfall traps was established. Each trap was at least 15 m distant from adjacent traps to insure independent samples (Digweed et al. 1995). Traps were 1L cylindrical plastic containers with diameters of 10 cm and a depth of 15 cm. Traps were dug in flush to the ground, and each was covered with a small wood roof raised about 3 cm from the ground, as described by Spence and Niemelä (1994).

Traps were filled with ethylene glycol as a preservative and emptied every two weeks. Sampling began on May 17th and continued to August 23rd, 2000 for a total of 7 sampling periods. Trap catches were standardized to 84 trapping days. Standardized catches of activity density from each trap were then pooled in each site, giving a standardized season total.

3.2.4 Data analysis

To assess similarity of native carabid assemblages, rank-abundance curves calculated from standardized species activity density data were used, basing rank order on catch in the rural assemblage. Differences in relative activity of greater than 10% between gradient positions or where a species made up at least 5% in one gradient position and 0% in another were considered significant and will be discussed with respect to this analysis.

Flight ability of native carabids was also assessed. Carabid species were classified, according to Lindroth (1961-69), as macropterous (having fully reflexed

wings), brachypterous (having vestigial wings) or dimorphic (a mixture of macropterous and brachypterous individuals). Macropterous and dimorphic carabids with wings considered by Lindroth (1961-69) to be too weak to sustain flight were considered to have the same low dispersal power as brachypterous species. The percentages of the total activity density of native species in all 3 wing-length categories were analyzed using a 3-way ANOVA with habitat type, gradient position and wing type as factors.

Species richness was taken as the total number of species captured at each site. Species diversity was calculated using both the Shannon-Weiner index, and Simpson's index (according to Pielou 1975). Both Simpson's and Shannon-Wiener index were used to assure a wide view of species diversity; the former is more sensitive to the dominant species and the latter to rare species (Sit and Taylor, 1998). Species evenness was calculated using the J function (Pielou 1975). The standardized season total catch at each location was used to calculate the indices and the values obtained were analyzed with a two-way ANOVA using gradient position and habitat type as factors. Activity density was taken as the standardized season totals of captures at each site and the data were analyzed using a two-way ANOVA with gradient position and habitat as factors. In order to assess the effects of introduced species on these assemblage characteristics, most analyses were performed both including and excluding introduced species.

3.3 RESULTS

Overall, 18 native species were captured in the grasslands and 12 were trapped in graveyards (Tables 3.2 & 3.3). The same 3 introduced species, *Carabus*

granulatus Linne, *Carabus nemoralis* Muller, and *Pterostichus melanarius* Illiger were captured in grasslands and graveyards. Of the 18 native species captured in grasslands, 10 were common (catch of species greater than or equal to 5% total catch of native species in one gradient position) and 8 were uncommon (< 5% of total). In the graveyards, 9 of the 12 native species were common and 3 species were uncommon.

Catches of 11 native species generally spanned the gradient, but 3 uncommon species were confined to rural areas (Tables 3.2 and 3.3). These were *Agonum sordens* Kirby, and *Patrobus foveocollis* Eschscholtz, found only in rural grasslands, and *Harpalus reversus* Casey, found only in rural graveyards. Two species uncharacteristic of open habitats, *Badister obtusus* Leconte, and *Agonum retractum* Leconte, were collected only in urban grasslands. Six native species were not found in any of the urban samples (Tables 3.2 and 3.3).

3.3.1 Gradient Patterns of Diversity and Abundance

Urbanization was associated with a significantly reduced number of carabid species present in a site (Fig. 3.2). With and without introduced species in the analysis, gradient position (with: $F = 3.5$, $df = 2, 18$, $P = 0.054$, without: $F = 3.8$, $df = 2, 18$, $P = 0.042$) explained number of species, without significant interaction with habitat type ($P = 0.507 - 0.603$). In both analyses, species number decreased with increasing urbanization. The grassland fauna included more native species than the graveyard assemblage ($F = 14.5$, $df = 1, 18$, $P = 0.001$) and more species overall ($F = 17.7$, $df = 1, 18$, $P = 0.001$, with introduced species).

The diversity of common species, as measured by Simpson's index, showed no response to urbanization with or without introduced species included in the analysis (i.e., gradient position or gradient x habitat [P = 0.077 – 0.891]), or habitat type (P = 0.445 – 0.941).

However, the Shannon-Wiener index of diversity, which amplifies effects of uncommon species, showed significant responses to the level of urbanization in both grassland and graveyard carabid assemblages (Fig. 3.3). Thus, uncommon species largely structure the results about species diversity. With introduced species excluded from the analysis, urbanization had a significant effect on this index ($F = 3.9$, $df = 2, 18$, $P = 0.039$) (Fig. 3.3), with no significant interaction term ($P = 0.343$). This resulted in a pattern of decreasing diversity with increasing urbanization for native assemblages in both habitats. This mirrors the patterns of the species totals for the native assemblages.

The Shannon-Wiener index also followed the pattern for raw species totals, with respect to habitat differences. Diversity of rare native species was significantly higher in the grasslands than in the graveyards ($F = 9.2$, $df = 1, 18$, $P = 0.007$) (Fig. 3.2). With introduced species included in these analyses, the effect of urbanization ($P = 0.579$) on assemblage diversity was insignificant. The interaction between gradient and habitat ($F = 3.4$, $df = 2, 18$, $P = 0.058$) was marginally insignificant. The Shannon-Wiener index for diversity of rare species, that included the introduced taxa, did not differ between the two habitat types ($P = 0.746$), emphasizing the homogenizing effect of introduced species on the carabid fauna.

With introduced species excluded, the J function was significantly affected by the interaction between habitat and gradient ($F = 4.3$, $df = 2, 18$, $P = 0.030$). This indicates a significant difference between the habitats in response patterns of the native carabid assemblages to urbanization. Evenness of native species decreased with increasing urbanization in graveyards (Fig. 3.4), while in grasslands, J increased with increasing urbanization. Native species assemblages were more even in grasslands than in graveyards ($F = 4.9$, $df = 1, 18$, $P = 0.039$). With introduced species included in the analysis of evenness, however, neither gradient, habitat nor their interaction were significant ($P = 0.126 – 0.959$).

The overall activity-density of carabid species showed a response to urbanization (Fig. 3.5). With introduced species included, neither gradient position nor the habitat x gradient interaction were significant ($P = 0.138 – 0.385$). This indicates that the activity-density of the entire assemblage, primarily made up of introduced species, is not significantly affected by urbanization. However, activity-density was highest in suburban areas and higher in rural areas than in urban, for the entire assemblage. With analysis restricted to native species the effect of urbanization was significant ($F = 6.7$, $df = 2, 18$, $P = 0.007$), but the interaction was not significant ($P = 0.220$). Activity-density of carabids was higher in the grasslands than in graveyards, both with ($F = 6.1$, $df = 1, 18$, $P = 0.024$) and without ($F = 6.0$, $df = 1, 18$, $P = 0.025$) introduced species.

3.3.2 Distributions of Introduced and Native Species

Eleven native species were shared by grassland and graveyard assemblages, representing 74% of the native species catch at grassland sites and 99% of the catch at

graveyard sites. One native species (*Harpalus reversus* Casey) was found only in graveyards, and 7 native species were restricted to grasslands in the samples (Tables 3.2 and 3.3).

The three introduced species (Fig. 3.6) numerically dominated the pooled fauna of grasslands and graveyards (% of catch: grassland, 85%; graveyards, 79%) and were all reasonably abundant in urban and suburban habitats. *Pterostichus melanarius* was also frequently captured in rural habitats and was the most abundant beetle species in the sample material overall. A few individuals of *C. granulatus* were found in rural habitats as well, but *C. nemoralis* was captured only in urban and suburban sites.

Contrary to expectations, based on degree of habitat similarity, native carabid assemblages differed more along the gradient in graveyards than in grasslands. This is illustrated by rank-activity-density curves (Tables 3.2 , 3.3, & 3.4, Fig. 3.7). In grasslands, 4 species exhibited greater than 10% differences in percent of activity-density among gradient positions; and 5 native species, common (5% of catch or greater) in one gradient position, were absent from another. The remaining 9 native species differed little in activity-density between positions, thus exhibiting a consistent core of native species.

In contrast, for native species trapped in graveyards, 3 of 12 exhibited greater than 10% differences in activity-density among gradient positions; 6, common in one position, were absent from another; and only 3 native species were characterized by roughly similar activity-density along the gradient. Thus, graveyards did not support a consistent group of core native species, and further this habitat configuration is not

likely to be central to the niche of any species. Beetles present at any one graveyard seemed more likely to have come from the surrounding landscape, rather than from populations reproducing in the graveyard itself.

3.3.3 Wing Morph Frequencies

As expressed by percent activity-density, in grasslands, individuals of native carabid species were distributed rather evenly over the three wing-length classes, but individuals of flightless species were somewhat more common, representing 39% of those captured (Fig. 3.8). Although the native grassland assemblage is dominated in number of species by macropterous (8 species) and dimorphic (6 species) carabids, in terms of individuals 2 common native flightless species (*Calathus ingratus* Dejean, and *Amara cupreolata* Putzeys) and to a lesser extent two rare native flightless species (*Patrobus foveocollis*, and *Poecilus lucublandus* Say) (Lindroth 1961-69) dominated (Tables 3.2).

In contrast, the graveyard carabid fauna was dominated by individuals of macropterous and dimorphic species (88% of native individuals), and included significantly fewer individuals of brachypterous carabid species (12%) ($F = 4.69$, $df = 2, 48$, $P = 0.014$) (Fig.3.8). The much lower values for activity density of flightless species in graveyards suggests that, for maintenance of these assemblages in graveyards, immigration by flight is more important than local recruitment.

3.4 DISCUSSION

3.4.1 Differences of Carabid Assemblages Between Habitats

The first goal of this study was to determine differences in carabid assemblages between grassland and graveyard habitats, and to identify habitat

characteristics that could promote such differences. I did not expect to find that graveyards and grasslands harbor permanent breeding populations of different carabid species. Instead, I predicted that they should be dominated by carabid species generally associated with open, early successional habitats with a large proportion of them being capable of flight. Most importantly, I expected to find a consistent core of native species in all gradient positions. Because graveyards appear to vary little in habitat quality, I expected their assemblages to be more homogenous than in grasslands, and that permanent populations of some species, dependent on habitat features absent in graveyards, would be missing.

Contrary to the prediction, the more carabid assemblages were likely affected by the landscape (graveyards), instead of local differences in habitat quality (grasslands), the greater were the differences in the assemblage of native species at each point along the gradient. Graveyards had no consistent core carabid fauna of their own, and thus species assemblages were composed mainly of invaders from surrounding habitats. With apparently no local populations, graveyard carabid faunas were completely dependant on immigration, which turned out the be the major effect of the landscape differences.

Native carabid species that are common in grasslands, as expected, are apparently influenced both by landscape effects and differences in habitat quality. Grasslands had a distinct core carabid fauna that extended the length of the gradient, but also included carabids from neighbouring habitats as well as species favoured by specific characteristics of each grassland.

Graveyards do not have their own distinct core fauna of native carabid species, as indicated by the lack of consistency in assemblages among the sites. This inference is supported by the fact that graveyards were dominated by macropterous and dimorphic carabid species, which are able to recolonize disturbed areas by flight. In urban graveyards, apparently only carabids that can fly to recolonize these sites persist, as 92% of the individual native carabids belonged to macropterous species. This argument is further strengthened by the fact that the only species found in urban graveyards, not found in either suburban or rural graveyards was *Pterostichus adstrictus* Eschscholtz, a macropterous forest-adapted species. This was probably because patches of aspen forest were the closest and most frequent source for urban graveyards. *Pterostichus adstrictus* had opportunity to inhabit these sites, whereas the closest and most frequent source patches for suburban and rural graveyards was farmland.

In contrast, grasslands have more similar carabid assemblages along the gradient than do graveyards and grasslands supported a significant proportion of brachypterous carabids (39% of individuals). These brachypterous beetles likely represent recruits from local (i.e. grassland) breeding populations. Overall, however, most of the species trapped in grasslands and graveyards were macropterous or dimorphic, emphasizing the probable importance of recurrent colonization for beetle populations in these open habitats, which are typical of early successional stages.

Carabid assemblages of graveyards are a random subset of the grassland carabid fauna living in the same areas. Only *Agonum placidium* Say, a widespread species, found in grasslands, was trapped more abundantly in graveyards. Only one

uncommon species trapped in graveyards was not found in grasslands, while the other 99% of individual carabids caught in graveyards belonged to species that were also found in grassland habitats. Therefore, graveyard assemblages are not distinct from grassland assemblages in the same localities.

3.4.2 Distribution of Native Carabid Assemblages

The carabid assemblages found in rural grasslands in this study differ conspicuously from an assemblage found in a small (c. 0.6 ha) meadow surrounded by aspen forest approximately 80 km northwest of Edmonton at George Lake (Niemelä et al. 1992). The latter assemblage included a total of 46 species: 7 were common and 39 were uncommon. Only 8 species were shared between the meadow at George Lake and the grassland assemblages of this study. Four common species were shared between the meadow and the rural grassland assemblages studied here. The other 4 shared species were uncommon in the meadow, but were common in the rural grasslands surrounding Edmonton.

The comparison of the fauna of the rural grasslands in this study and that of the prior study at George Lake suggests three conclusions. First, grassland assemblages vary a great deal, depending on the locality; second, the fauna at the George Lake meadow (1981-82) appears to have been much more speciose than habitats studied here; and third, the carabid assemblages of the grasslands surrounding Edmonton are a markedly limited representation of the Central Alberta fauna.

When the study by Niemelä et al. (1992) was completed, *P. melanarius* was absent from the George Lake fauna. In the laboratory, *P. melanarius* has a negative

effect on a smaller carabid species (e.g. *Pterostichus adstrictus* Eschsholtz) via interference competition (Currie et al. 1996). Most native species reported from the meadow at George Lake were the size of *P. adstrictus* or smaller (Lindroth 1961-69). It is possible that the high activity density of *P. melanarius* around Edmonton is causally associated with the lower diversity of grassland carabids. An alternative hypothesis would be that the higher diversity at George Lake might reflect the lower level of anthropogenic disturbance in the meadow than is probable in the rural grasslands in this study. Disturbance has been shown to have a consistently negative effect on diversity of higher trophic level species, such as carabids (Putman, 1996) and may explain why there are more common and fewer uncommon species in the rural grassland sites than at the George Lake meadow. These hypotheses can be tested through repeated sampling as exotic species move into areas with good records of pre-contact carabid assemblages.

3.4.3 Characteristics of Native Carabid Assemblages

Differences in assemblage characteristics between grasslands and graveyards appear to be attributable mainly to differences in habitat quality as the sites were subject to the same landscape conditions. Although a landscape component to the higher diversity in urban grasslands compared to urban graveyards could be due to the proximity of the former to the river valley greenspaces, diversity was also higher in the suburban and rural grasslands than in suburban and rural graveyards, which were much closer to good beetle habitat. The higher diversity in grasslands may be simply due to the complexity of the habitat (Davis, 1980). The structure of tall, leafy plants, for example, creates greater variation in microhabitats. In addition, the higher

levels of local disturbance in graveyards should affect diversity negatively (Davis, 1980). Rare species contributed greatly to the higher number of species in grasslands. The species that occurred in suburban and rural grasslands but not in suburban and rural graveyards were likely absent from the latter habitat due to the fact that grasslands are suitable for more species. Therefore more species were likely to stay either permanently or for a period of time in grasslands to exploit resources so they were more likely to be trapped there.

Higher disturbance rates locally should increase the populations of a few species and more than compensate for the loss of populations of other species. This should result in a higher local assemblage density (Chudzicka and Skibinska 1994, Schaefer 1980), which should translate into a higher activity density. Habitats with high disturbance rates favour opportunistic species, especially dietary generalists. With ample resources (prey should follow the same patterns) and low diversity of resources coupled with few competitors these species populations that exploit these resources should flourish. However, activity-density was greater in the less directly disturbed grasslands than in the graveyards. This indicates that either the grasslands have a higher or more diverse resource base for beetles, or more likely, that the regular disturbances typical of graveyards have a negative effect on both activity density and diversity of the resident beetles.

3.4.4 Partitioning Gradient Patterns

The second goal of this study was to identify gradient effects on assemblages of grassland carabid beetles. I expected that urban and suburban habitats should have assemblages more similar to those in earlier successional stages or in highly disturbed

habitats than rural sites (Strueve-Kusenberg 1980, Gray 1989), reflecting change in response to the degree of urbanization. Three predictions follow. First, more urbanized environments should be associated with lower diversity. Second, more opportunistic species, such as many introduced species, should occur in urban areas as found in previous studies of carabids and of other taxa (Karr 1998, Airola and Buchholz 1984, Spence and Spence 1988, Niemelä and Spence 1991). Third, urban areas, although dominated by a few opportunistic common species, should have higher overall activity density.

The third goal of the study was to partition the effects of landscape patterns and habitat quality on carabid assemblages. I predicted that gradient patterns in graveyard carabid assemblages would reflect mainly landscape effects because habitats are so homogeneous (ecologically monotonous). Grassland assemblages, then, should reflect both landscape and habitat effects, and would be relatively richer, because of habitat variation. As the third goal of the study is linked to the success or failure of the second goal the two goals will be discussed in concert.

Patterns in grassland assemblages that match patterns in graveyard assemblages (i.e., absence from graveyards of specialists and rare species) should be reasonably attributed to chiefly landscape level disturbances (Gray 1989, Strueve-Kunsenburg 1980), such as habitat fragmentation and its effects on immigration. Patterns found in the grassland assemblages that do not match the patterns found in the graveyard assemblages (e.g., loss of the loss of specialists and rare species in graveyards) can reasonably be attributed to differences in habitat quality such as degree of habitat simplification (Davis 1978). Both habitats are open and have

similar carabid fauna, so the effects of landscape should be similar in the assemblages in both habitats, and differences in responses may be attributed to effects of habitat quality. To put it another way, all patterns found in graveyard assemblages may be considered as landscape-based effects. As the landscape surrounding the different habitats is very similar at each respective gradient position, then the causal factors of these patterns of landscape effects should exert consistent effects on each habitat. When patterns are found in a habitat that varies in local quality, these patterns are most likely due to the differences in habitat quality along the gradient. Conspicuous patterns in diversity depended mainly on rare species. Both the Shannon-Wiener index and raw species numbers decreased with increasing urbanization, reflecting mainly changes in the diversity of rare native species. The decrease in species diversity associated with increasing urbanization in graveyards, a habitat with minor variation in habitat quality variation, appears to be mainly an effect of the surrounding landscape leading to less immigration in urban areas. The fragmented habitat matrix surrounding the urban sites (and suburban sites to some degree) contains mostly impermeable ground with little or no litter or plant layer (asphalt and concrete), which likely supports a low carabid abundance and diversity. This in turn leaves mainly species that can migrate longer distances (as shown by the wing morph data earlier) from other patches of favourable habitat to be able to visit or colonize these urban habitats along with the few species that persist in the marginal habitat. The drop in diversity, also found in urban grassland assemblages, must also reflect this constraint and could be easily related to a generally increased amount of disturbance in urban sites surrounding these habitats (Gray 1989, Trojan 1994).

Urban and suburban areas experience continuous and prolonged disturbances (Niemelä et al. 2002). Such disturbances could simply eliminate species with long-lived populations characterized by low density.

Evenness varied significantly across the gradient for the native carabid assemblage, only. In graveyard assemblages, evenness tended to decrease with increasing urbanization although effect of gradient position was only marginally significant. This modest difference could reflect increased dominance of a few eurytopic and opportunistic species with increased levels of disturbance and urban isolation. In grassland assemblages, the pattern was opposite: evenness increased with increasing urbanization. It is reasonable to conclude that differences in local habitat quality override the effect of the landscape along the gradient in the structurally richer grasslands. In short, urban grasslands likely supported breeding populations of a consistent core group of species and their consistent success relative to that of rarer species with more specialist habits led to greater evenness in urban habitats.

For the pooled assemblage of native species, activity-density differed significantly according to gradient position. In the grasslands and graveyards activity-density of native species was greater in the rural areas (grasslands: rural > 4 times urban, graveyards: rural > 6 times urban) than in the urban sites. The patterns in activity-density along the gradient including introduced species, while not statistically significant, are similar.

These results are the opposite of what has been found in previous gradient work and other studies of urban areas (Chapter 1, Niemelä et al. 2002; Spence and

Spence 1988) including a study done in vacant lots (McIntyre 2000), similar to urban grasslands in this study. Rural sites are unlikely to support larger, local populations (reflecting better habitat quality), as graveyards do not appear to vary enough in habitat quality to account for the differences in activity densities. I suggest that agricultural landscapes surrounding rural sites, which support high densities of carabids (Cárcamo, Niemelä and Spence 1995), act as a source of beetles for both grasslands and graveyards and the changes in average abundance seen along the gradient are caused mainly by landscape effects related to this imbalance. What is even more surprising and somewhat inexplicable, was that activity densities of native carabids were highest in suburban areas in both grasslands and graveyards.

The natural history of the species (Lindroth 1961-69) captured in either grasslands or graveyards provides no obvious explanation for the differences in site occupancy discovered in this study. The species that differed in abundance along the urban-rural gradient are, in general, considered to be common in dry to moist, open habitats with vegetation ranging from sparse to thick. Species associated with weeds occurred in urban, suburban, and rural sites. The presence of one supposively strictly forest species (*Badister obtusus*) is easily explained, as it was found in only one urban site (PRM) that was surrounded by forest. A single species captured in graveyards, *P. pensylvanicus*, is generally associated with forest. Its presence in sizable numbers in rural graveyards was surprising as little forest was adjacent. This underscores the variable and haphazard nature of carabid assemblages of graveyards.

3.4.5 Conclusions

The native carabid fauna of grasslands and graveyards included mostly open habitat specialist species. Many of the species were macropterous and wing-dimorphic. Only in grassland habitats were some brachypterous species common, suggesting local recruitment of a consistent core of resident species. Diversity and activity density were greater in grasslands than in graveyards, possibly due to greater habitat complexity.

I reasoned that patterns of species evenness and structure of native carabid assemblages responded to variation in habitat quality. Overall, however, effects of landscape seem to account for more of the patterns observed. Patterns in diversity of rare species, carabid activity density and the structure of the introduced carabid assemblage were better explained by landscape factors than variation in habitat quality. Thus, conservation of urban faunas will likely depend on considerations in addition to provision for a few relatively small park areas.

Two of three predictions about the impact of the urban-rural gradient on carabid assemblages were corroborated. Higher diversity in rural assemblages likely was due, in part, to negative influences flowing from the urbanized landscape. Also, more introduced species were in urban areas. This could reflect a positive effect of urbanization on these species or simply be a historical consequence of where the exotic species were first established (Spence and Spence 1988). Activity density, however, was higher on the rural end of the gradient and did not follow predictions based on previous work in other habitats. This may reflect movement of beetles into small grassland patches from surrounding farmlands.

Table 3.1. List of Grassland and Graveyard Sites. Classification, names and designation of sites where pitfall traps were installed on Edmonton-Elk Island National Park urban-rural gradient. (Abrvn = Abbreviation)

Habitat &Gradient Position	Site Name	Abrvn	Location
Grassland			
-Urban	On Victoria Trail	VTL	South side of Victoria Trail
	Provincial Museum	PRM	In the river valley south of museum
	Shaw Conference Center	SHW	North of the parking lot
	Edmonton Queen Dock	EDQ	Southwest from the parking lot
-Suburban	Superstore	SUP	142 Ave and 127 Street
	Holiday Inn	HLI	100 Ave and 179 Street
	Oxford housing development	OXF	153 Ave and 127 Street
	70th and 17th street	SEV	70 Ave and 17 Street
-Rural	Rural grassland-1	RG-1	North of TWP542 and on RR220
	Rural grassland-2	RG-2	Just north of the EINP north gate
	Rural grassland-3	RG-3	South of TWP560 and on RR180
	Rural grassland-4	RG-4	North of TWP552 and on RR180
Graveyards			
-Urban	Mount Pleasant	MTP	Easily found on a city map
	Edmonton City	EDM	"
	Beechmount	BCH	"
	Jewish Community	JWC	"
-Suburban	Our Lady of Peace	OLP	"
	Holy Cross	HLC	"
	Little Mountain	LTM	"
	Colchester	COL	SW-10-52-23
-Rural	Bethany Lutheran	BTH	On RR 205 and TWP540
	Lamont United	LMT	East of Lamont on HWY637
	Saint Nicholas	STN	East of RR182 on TWP560
	Saint Michaels	STM	North of TWP564 on RR190

Table 3.2. Species List of Grassland Carabid Assemblages. Species list of grassland carabid assemblages, native species rank (from rural activity density), classification of rare versus common species, gradient positions found at, and wing length across the Edmonton-Elk Island National Park urban-rural gradient. (* = introduced species), (U = urban, S = suburban, R = rural), (Macropterous = fully reflexed and flight capable, Brachypterous = vestigial and incapable of flight, Dimorphic = mixture of Brachypterous and Macropterous individuals), (# = wings incapable of flight), (! = a few rare macropterous specimens exist)

Species Name	Native Species Rank	Status	Gradient Position	Hind Wings
Carabus granulatus Linné*	N/A	N/A	U, S, R	Brachypterous
C. nemoralis Müller*	N/A	N/A	U, S	Brachypterous
Pterostichus melanarius Illiger*	N/A	N/A	U, S, R	Dimorphic
Calathus ingratus Dejean	1	Common	U, S, R	Brachypterous!
Harpalus fulvilabris Mannerheim	2	Common	U, S, R	Dimorphic
Amara cupreolata Putzeys	3	Common	U, S, R	Macropterous#
Amara littoralis Mannerheim	4	Common	S, R	Macropterous
Agonum cupreum Dejean	5	Common	U, S, R	Dimorphic
Pterostichus adstrictus Eschscholtz	6	Common	U, S, R	Macropterous
Cymindis cribricollis Dejean	7	Common	S, R	Dimorphic
Patrobus foveocollis Eschscholtz	8	Uncommon	R	Brachypterous
Agonum sordens Kirby	9	Uncommon	R	Macropterous
Pterostichus pensylvanicus Leconte	10	Uncommon	S, R	Dimorphic
Amara ellipsis Casey	11	Common	U, S, R	Macropterous
Amara torrida Leconte	12	Common	U, S, R	Macropterous
Agonum placidium Say	13	Uncommon	U, S, R	Macropterous
Poecilus lucublandus Say	14	Common	U, S, R	Macropterous#
Chlaenius purpuricollis Randall	15	Uncommon	S, R	Macropterous
Synuchus impunctatus Say	16	Uncommon	S	Dimorphic
Badister obtusus Leconte	17	Common	U	Macropterous
Agonum retractum Leconte	18	Uncommon	U	Dimorphic

Table 3.3. Species List of Graveyard Carabid Assemblages. Species list of graveyard carabid assemblages, native species rank (from rural activity density), classification of rare versus common species, gradient positions found at, and wing length across the Edmonton-Elk Island National Park urban-rural gradient. (* = introduced species), (U = urban, S = suburban, R = rural), (Macropterous = fully reflexed and flight capable, Brachypterous = vestigial and incapable of flight, Dimorphic = mixture of Brachypterous and Macropterous individuals), (# = wings incapable of flight), (! = a few rare macropterous specimens exist)

Species Name	Native Species Rank	Status	Gradient Position	Wing Length
Carabus granulatus Linné*	N/A	N/A	S	Brachypterous
C. nemoralis Müller*	N/A	N/A	U	Brachypterous
Pterostichus melanarius Illiger*	N/A	N/A	U, S, R	Dimorphic
Agonum cupreum Dejean	1	Common	S, R	Dimorphic
Agonum placidium Say	2	Common	U, S, R	Macropterous
Harpakus fulvilabris Mannerheim	3	Common	S, R	Dimorphic
Cymindis cribricollis Dejean	4	Common	R	Dimorphic
Pterostichus pensylvanicus Leconte	5	Common	R	Dimorphic
Poecilus lucublandus Say	6	Common	R	Macropterous#
Amara cupreolata Putzeys	7	Common	U, R	Macropterous#
Calathus ingratus Dejean	8	Uncommon	R	Brachypterous!
Harpalus reversus Casey	9	Uncommon	R	Macropterous
Amara ellipsis Casey	10	Common	S, R	Macropterous
Synuchus impunctatus Say	11	Uncommon	R	Dimorphic
Pterostichus adstrictus Eschscholtz	12	Common	U	Macropterous

Table 3.4. Rank-Activity-Density Differences Along Grassland and Graveyard Gradient. Summary of the differences in native carabid species assemblages along the urban-rural gradient as measured by activity-density.

Native Species	Grasslands	Graveyards
Total Number of Species	18	12
Number of species with more than 10% differences in values for activity-density along gradient	4 species. = 22% of total number of species	3 species. = 25% of total number of species
Number of species common in one gradient position and absent from another	5 species. = 28% of total number of species	6 species. = 50% of total number of species
Number of species differing little in activity-density along the gradient	9 species. = 50% of total number of species	3 species. = 25% of total number of species

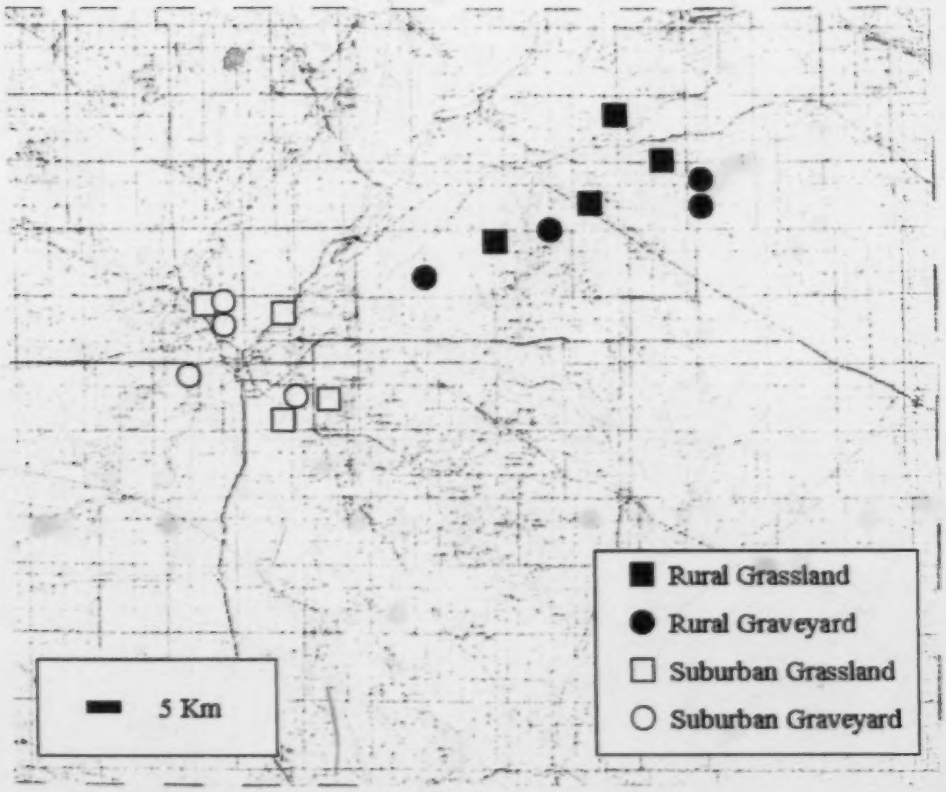


Fig. 3.1. Map of Graveyard and Grassland Gradient. Map of suburban and rural, graveyard and grassland sites. Urban sites were not included as there would be very little space between them. Source: Canadian Department of Mines and Technical Surveys

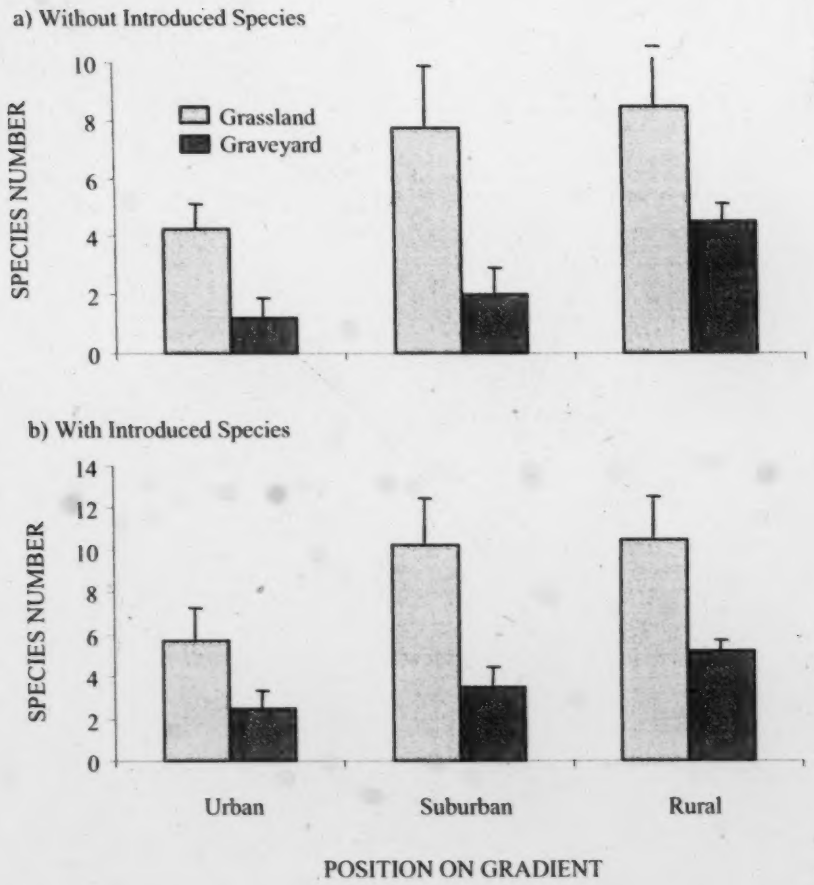


Fig. 3.2. Species Number Per Site Along Graveyard and Grassland Gradient. Species number per site for grasslands and graveyards both a) without and b) without introduced species. Standard error bars included.

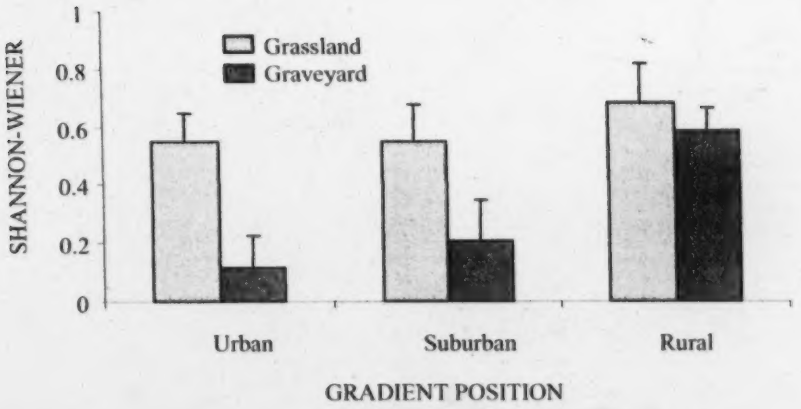


Fig. 3.3. Shannon-Wiener Estimates of Diversity Along Graveyard and Grassland Gradient. Shannon-Wiener index along the gradient for grassland, and graveyards without introduced species included in the assemblage. Standard error bars included.

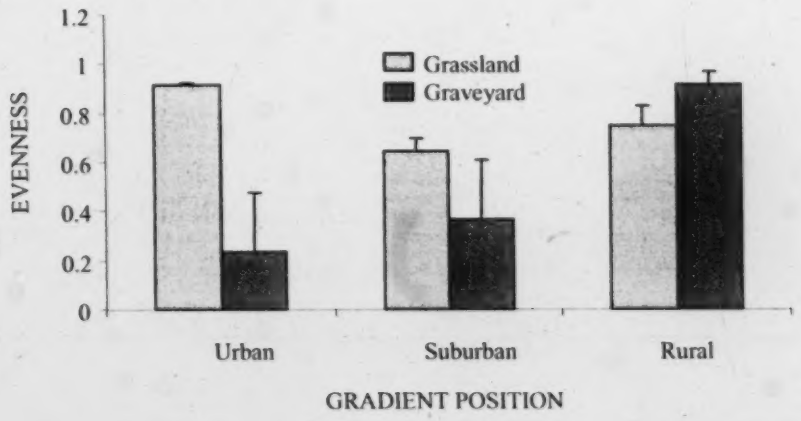


Fig. 3.4. Species Evenness Along Graveyard and Grassland Gradient. J function (species evenness) along the gradient for grasslands, and graveyards without introduced species included in the assemblages. Standard error bars included.

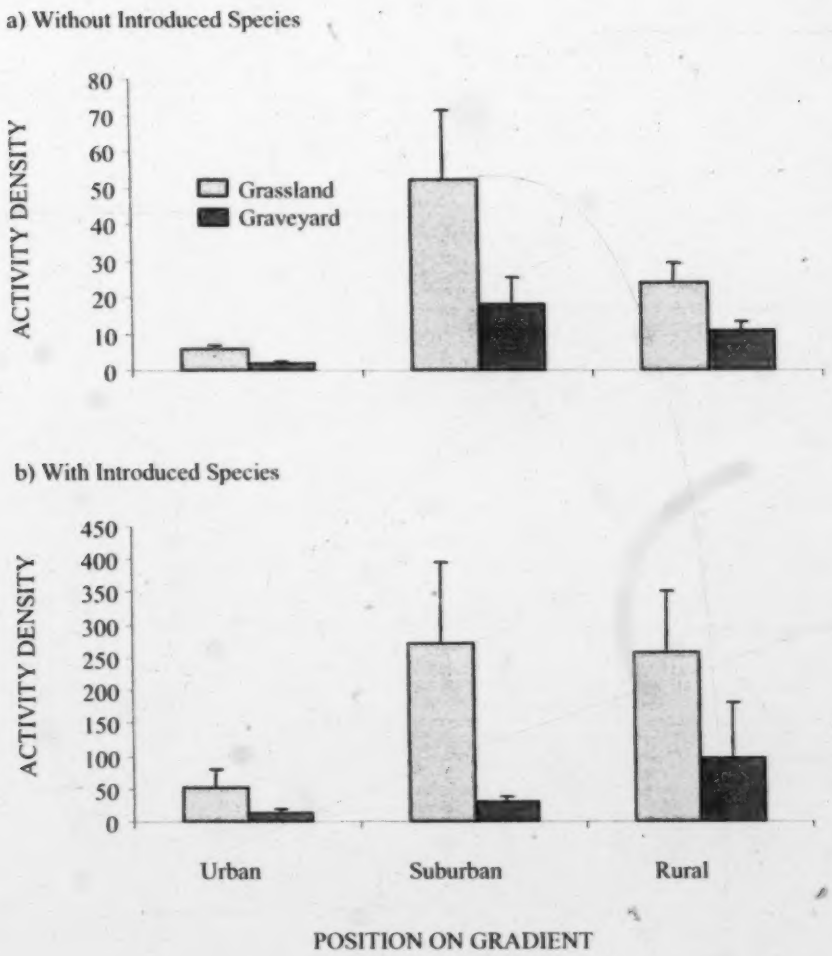


Fig. 3.5. Total Activity-Density Along Graveyard and Grassland Gradient. Standardized activity density along the gradient for grassland, and graveyard a) without and b) with introduced species included in the assemblage. Standard error bars included

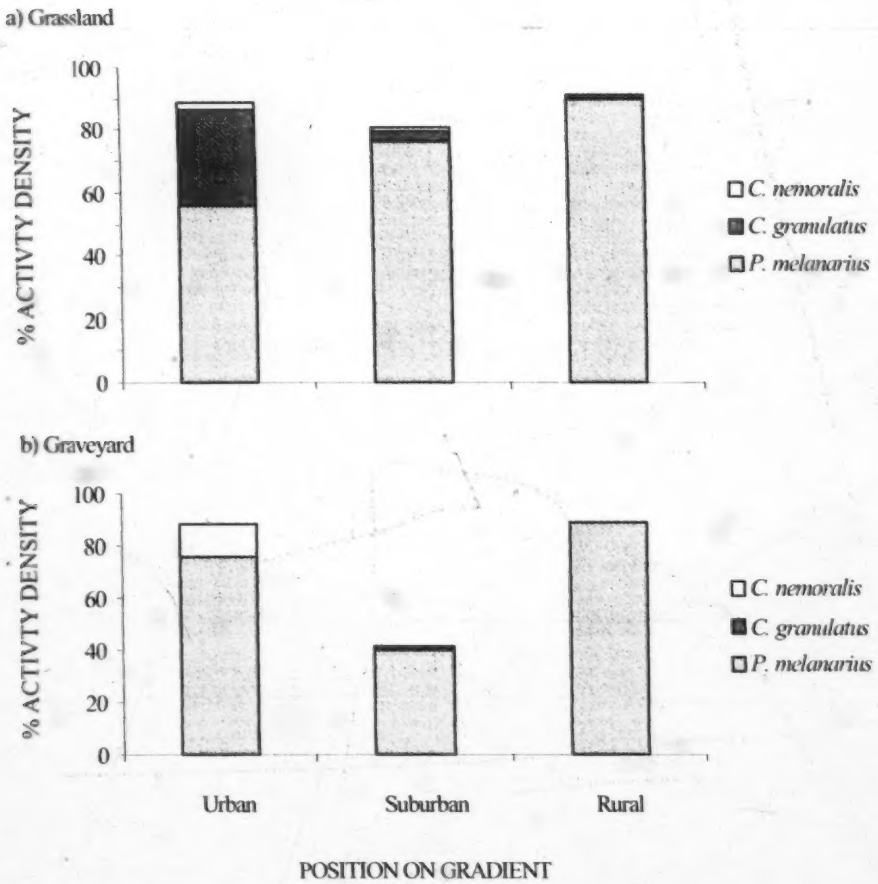


Fig. 3.6. Introduced Species Activity-Density Along Graveyard and Grassland Gradient. Activity density (number of individuals captured per 84 trap days) of introduced species as percent of total standardized catch for a) grasslands, and b) graveyards.

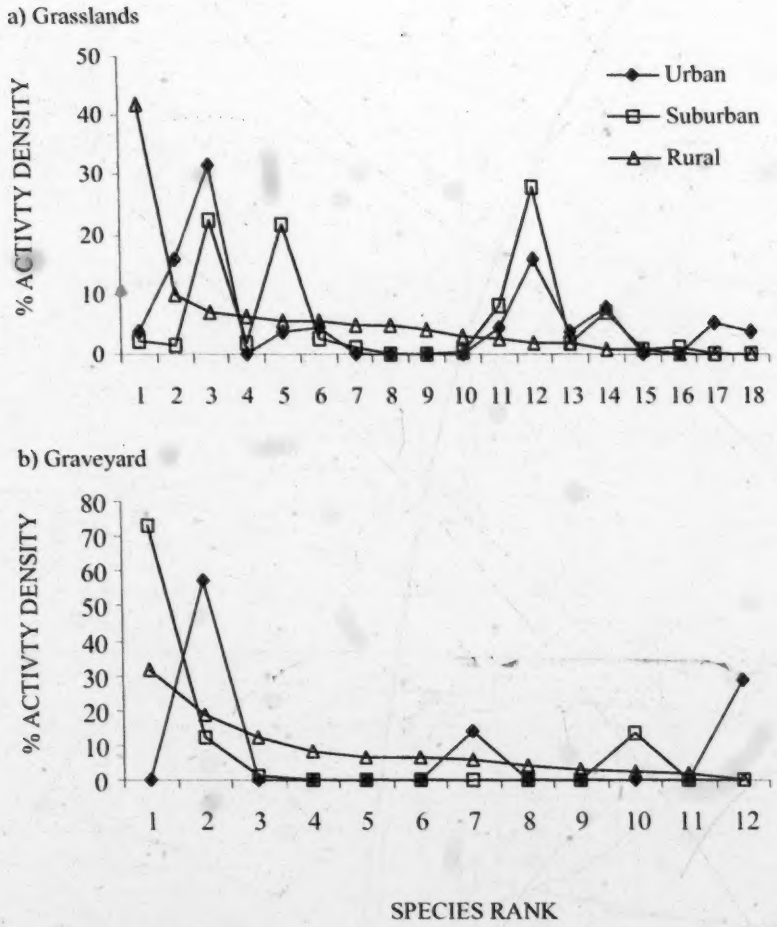


Fig. 3.7. Rank-Abundance of Native Species Along Graveyard and Grassland Gradient. Rank-abundance of native species activity density expressed as percent of standardized catch for a) grasslands and b) graveyards. Rank was held consistent at that established by rural activity density of species. Numbers on X-axis represent species captured. For names, see Tables 3.2 and 3.3.

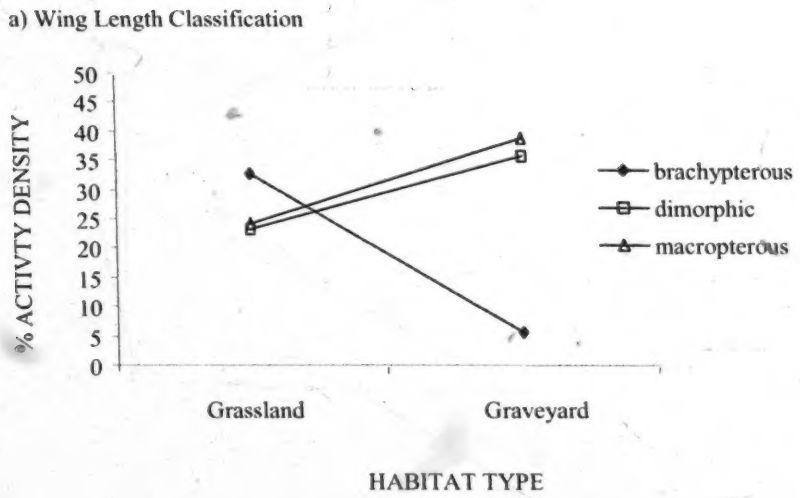


Fig. 3.8. Wing Length Classification of Native Species Along Graveyard and Grassland Gradient. Cross-habitat comparisons for wing length classification of native species.

CHAPTER FOUR

4.1 CONCLUSIONS

4.1.1 Research Summary

The main goals of Chapter 2 were to discover gradient effects on carabid assemblages in aspen forest along the urban-rural gradient and to discover what effect introduced species were having on the native carabid fauna. The analyses of the native carabid community, alone did not show effects on diversity, evenness or activity density. Results did hint at possible negative effects of urbanization on rare species diversity and positive effects on native carabid activity-density. With introduced species included in the analyses, however, effects of urbanization were significant. Diversity of both rare and common species decreased with increased urbanization, as did species evenness. Although the effect on overall activity-density of carabids was statistically insignificant, results for this variable suggested that urbanization had a positive effect. These effects may be due to variation in landscape or habitat quality, or both. These findings appear to have some generality across taxa as they corroborate previous empirical studies of carabids and stream fauna (Czechowski 1982; Karr 1998; and McIntyre 2000), and with theoretical models of populations in highly disturbed habitats (Strueve-Kusenberg 1980, Gray 1989)

Surmising that disturbance may be the driving factor of gradient effects in aspen forests, as seen in Chapter 2, I attempted to associate several measures of local and landscape level disturbance with measures of rare species diversity and activity-density. Landscape measures of disturbance were stronger predictors of diversity, while local level measures were weaker predictors. For activity-density, in contrast,

local disturbance measures were good predictors, while landscape level measures were poor predictors. So, in aspen forest, the lower diversity due to urbanization seems to be associated with landscape level factors, while the increased activity-density of urban habitats is better correlated with local disturbance.

In Chapter 3 the main goal was to discover for gradient effects on carabid assemblages in grassland and graveyard habitats along the urban-rural gradient, and to identify what effects were caused mainly by landscape variation and those caused by variation in habitat quality. Partly due to the more robust analysis supported by 2-way ANOVA, significant effects were found for the native carabid assemblage, only. The effect of increased urbanization on rare native species diversity was negative. This expected gradient pattern appeared to be a landscape effect. The evenness of the native assemblage increased with increased urbanization in grasslands. This unexpected gradient pattern appeared to be an effect of habitat quality. As urbanization, in general, should favour increased dominance of the assemblage by opportunistic species, due to increased disturbance, one would expect rural assemblages to have a more even distribution of common species than urban assemblages. In contrast to what was found in aspen forests, density, as measured by activity, of native carabid species decreased with increased urbanization in the open habitats. This unexpected gradient pattern appeared to be a landscape effect. While statistically insignificant, the effect of urbanization on the activity density of the entire carabid assemblage tended to be negative in both habitats.

In both aspen forests and grasslands, urbanization was positively associated with establishment of introduced species as more of them were found on the urban

end of the gradient. In grasslands, at least, this appeared to be an effect of the landscape. This is consistent with results of previous studies (Airola and Buchholz 1984, Spence and Spence 1988, Karr 1998)

A secondary goal for the study of the carabid assemblage of aspen forest was to gauge the progress of introduced carabid species invasions in the Edmonton area. Three introduced species; *Carabus nemoralis* Müller, *Carabus granulatus* Linne, and *Clivina fossor* Linne were restricted to urban and suburban sites. A fourth introduced carabid, *Pterostichus melanarius* Illiger, was established in all gradient positions. Data about wing morph frequencies (% long-winged individuals) of *P. melanarius* along the gradient suggest that urban populations were spatially stable (Den Boer 1970), with long-winged proportions of the populations almost as low as those reported for long-occupied habitats in Europe (Den Boer and Van Dijk 1996), while rural populations were made up of primarily macropterous individuals, inferred to be recent migrants. This indicates that *P. melanarius* is still expanding outward from Edmonton, whereas the ranges of the other introduced carabids are not expanding.

A secondary goal for the study of grassland and graveyard carabid assemblages was to seek out the differences between the two, and to determine whether or not the habitats were distinct, i.e., were the carabid assemblages of the habitats significantly different from each other and did each of the habitats support a consistent, core fauna, indicating the presence of persistent local populations? Graveyards had no consistent core of carabids; rather that assemblage was a subset of the species found in the grasslands. Thus, for carabids, graveyards habitats were not distinct from grassland habitats. Graveyards had lower diversity, species evenness,

and activity density than seen in grasslands. Increased complexity of habitat and lower local disturbance rates likely cause these differences in assemblage characteristics. The carabid fauna of grasslands and graveyards (especially) were dominated by species that were capable of flight, suggesting the importance of dispersal ability in colonizing these habitats. Graveyards, in particular, were nearly entirely made up of species with flight ability, and this suggests that the carabid fauna of graveyards consists of migrants, without long-term resident populations.

4.1.2 General Discussion

With gradient patterns of carabid assemblages in graveyards are considered as a baseline of landscape-based gradient patterns for all habitats along the gradient some interesting inferences may be made about the gradient patterns found in aspen forests. All patterns found in graveyard assemblages can be considered as landscape based effects. As the landscape surrounding the different habitats is very similar at each respective gradient position, then the causal factors of these patterns of landscape effects should exert consistent effects on each habitat. Different patterns found in a habitat that vary in local quality, then are most likely due to differences in habitat quality along the gradient. This may seem to be quite a jump in logic, but considering that the patterns of diversity and introduced species found in these studies mirror studies on completely different orders of insects occupying completely different niches, using completely different taxonomic levels, and in completely different habitat types in urban areas of North America (Karr 1998) there may be some validity in this.

Comparing the gradient patterns of carabid assemblages in aspen forest to those of graveyard assemblages, few gradient patterns match, and therefore can be considered as landscape-based. However, when data from the forest sites were included in the 2-way ANOVAs (after being standardized to the same number of traps and trapping days) with grassland and graveyard faunistic data, more landscape level responses (rare species diversity, species evenness, introduced carabid assemblage) than habitat quality responses are evident in the aspen forest assemblages.

Two responses in aspen forest remained based on differences in habitat quality. First, the gradient pattern for activity-density in aspen forest assemblages was opposite to that found in graveyards; and second, the native species assemblages in aspen had a consistent core fauna along the gradient, again unlike graveyard carabid assemblages. That activity density responded to variation in habitat quality is not surprising, as it was more strongly associated with local disturbance, which is a part of habitat quality. The differences in native species assemblage in aspen forest along the gradient and the increase in diversity, however, is not likely contributed only by differences in landscape. Many rare species found only in rural areas are likely present due to the synergy between the greater variety in habitat (local quality effects) and the greater continuity (landscape effects) of the rural aspen forest. The aspen forest exhibited higher rare species diversity and higher carabid activity density than did grasslands. These results may reflect the greater structural complexity of aspen forests and/or lower rates of local disturbance. With respect to differences in activity density, resources for the carabid assemblage may be more concentrated in

the aspen forest, and they may also be more diverse in aspen forest than in grasslands. Another explanation is that predation pressure on carabids may be less in forested sites. These are all factors of habitat quality.

Comparison of wing morph frequencies of *P. melanarius* between the habitats provided some surprising results. While urban aspen forest had the lowest frequencies of macroptery (long-wingedness), indicating the most spatially stable populations, rural forests had the highest frequencies. In fact the average of the rates of macroptery pooled across the gradient are counter intuitive as aspen forest had the highest rates of macroptery (31%), followed by grasslands (25%), then graveyards (21%). Thus, it appears that aspen forest, the habitat with the most variation of habitat quality, was in general the hardest to invade overall, with respect to carabids, as the invasion of all habitat types would have begun at the same time. The lowest rates of macroptery in *P. melanarius* populations were found in the urban sectors in all three habitats, adding more weight to the argument that urban habitats are generally first, or perhaps most easily, colonized by invasive species.

Regardless of habitat type, *P. melanarius* has invaded all gradient positions, in contrast to other introduced carabid species. One or more of three hypotheses may account for why *P. melanarius* has done so well. One of the most plausible is that *P. melanarius* has a greater dispersal capability compared to *C. nemoralis* and *C. granulatus* (Den Boer & Van Dijk 1996). Another is that *P. melanarius* arrived in Edmonton likely sometime in the mid to late 50's while *C. granulatus* arrived much later as may be surmised from the earliest capture records (however, it appears that *C. nemoralis* arrived before *P. melanarius*) (George E. Ball, personal communication).

A third possible but very general reason is that *P. melanarius* is either better adapted to the local niches or has encountered less environmental resistance (Niemelä and Spence, 1991).

Of several hypotheses about events in these communities, the simplest is that introduced species are filling empty niches (Peters 1977), which may be more extensive in the urban areas. Another possibility is that the native fauna is not resource-limited and therefore the species are not competing with one another (Niemelä and Spence 1991). A third and more complex possibility is that resource competition or direct interference competition may be occurring, but striking effects are not yet evident. The latter form of competition seems more likely as resources generally appear not to limit distributions of carabid species (Den Boer and Van Dijk 1996). The data from this thesis seem to suggest that in some habitats and gradient positions interference competition may occur, but in most sites the species do not appear to be competing with each other.

Populations of *P. melanarius* may be at near maximum abundance in urban aspen habitats due to their extreme activity density and low rate of macroptery, and therefore should not increase dramatically. If this is so, perhaps native populations will not decline further. The populations of *P. melanarius* outside the city are not yet spatially stable; they are unlikely to have become fully established and are likely to expand. The short-term effect on rural native populations will likely be negative.

4.1.3 Future Research

One line of useful future research on the urban ecology of carabids could lead to development of a tool to be used by city managers to gauge the success of past and

future management practices of urban greenspaces, with diversity of native species, and activity densities of introduced species providing a barometer for habitat integrity.

Research may also be conducted to determine if the patterns in carabids are reflected in other assemblages of ground dwelling arthropods, such as spiders, staphylinid beetles, centipedes, etc., so as to establish the possible generality of impacts. If responses of these groups reflect the same gradient patterns as the carabids then it would strengthen the argument that carabids are an indicator of habitat integrity.

Conditions associated with urbanization, such as physical environment, soil chemistry, litter decomposition, vegetation, etc., should be studied in concert with ground dwelling arthropod communities, in order to better understand and isolate what exact effects of the urban environment are responsible for the changes in these communities. This may lead to development of management strategies that promote the integrity of this community.

Finally, as argued by Pickett et al. (2001), urban ecology should expand its scope to integrate biological information with that from the social sciences. In this way it will be possible to more fully comprehend the interactions between the characteristics of the city land mosaic and the urban invertebrate fauna. The integration of social ecology of humans into insect studies may draw out some fascinating relationships and help us better understand what we are doing to the environment around us.

LITURATURE CITED

Airola, T.M. and K. Buchholz. 1984. Species structure and soil characteristics of five urban sites along the New Jersey Palisades. Urban Ecology 8:149-164.

Aukema, B., A.J. Spee, and TH.S. Van Dijk. 1996. Wing dimorphism and development in *Pterostichus melanarius* (Coleoptera: Carabidae). Ent. Ber. Amst. 56(6):93-100.

Bousquet, Y. and A. Larochelle. 1993. Catalogue of the Geadephaga (Coleoptera: Trachypachidae, Rhysodidae, Carabidae, including Cicindelini) of America north of Mexico. Memoirs of the Entomological Society of Canada 167: 397 pp.

Cárcamo, H.A., J.K. Niemelä & J.R. Spence. 1995. Farming and ground beetles: effects of agronomic practice on populations and community structure. The Canadian Entomologist 127:123-140.

Carter, A. 1976. Wing polymorphism in the insect species *Agonum retractum* Leconte (Coleoptera: Carabidae). Canadian Journal of Zoology 54:1375-1382.

Churcher, P.B., and J.H. Lawton. 1987. Predation by domestic cats in an English village. Journal of Zoology 212:439-455.

Chudzicka E., and E. Skibinska. 1994. An evaluation of an urban environment on the basis of faunistic data. Memorabilia Zoologica 49:175-186.

Currie R.C., J.R. Spence and J.K. Niemelä. 1996. Competition, cannibalism and intraguild predation among ground beetles (Coleoptera: Carabidae): a laboratory study. The Coleopterists Bulletin 50:135-148.

Czechowski, W. 1982. Occurrence of carabids (Coleoptera, Carabidae) in urban greenery of Warsaw according to the land utilization and cultivation. Memorabilia Zoologica 39:103-108.

Davis, B.N.K. 1978. Urbanisation and the diversity of insects. In: Diversity of Insect Faunas. Blackwell, London, UK. P. 126-138.

Davis, B.N.K. 1980. Habitat diversity and invertebrates in urban areas. In: Urban Ecology, Bornkamm, R., J.A. Lee, and M.R.D. Seaward (eds.). Blackwell, London. P. 49-64.

Den Boer, P.J. 1970. On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae). Oecologia 4:1-28

Den Boer, P.J. and T.S. Van Dijk. 1996. Life history patterns among carabid species. Tijdschrift voor Entomologie 139:1-16.

Desender, K., J.P. Maelfait, and L. Baert. 1991. Carabid beetles as ecological indicators in dune management. Elytron:239-247.

De Vries, H.H. and P.J. Den Boer. 1990. Survival of populations of *Agonum ericeti* Panz. (Coleoptera, Carabidae) in relation to fragmentation of habitats. Netherlands Journal of Zoology 40:484-498.

Digweed, S.C., C.R. Currie, H.A. Cárcamo, and J.R. Spence. 1995. Digging out the "digging-in effect" of pitfall traps: Influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiologia 39:561-576.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.

Erwin, T.L. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In: Ball, G.E. (ed), Taxonomy, Phylogeny, and Zoogeography of Beetles and Ants. Dordrecht, Junk, p.437-472.

Evans, M.E.G. 1990. Habits or habitats: do carabid locomotory adaptations reflect habitats or lifestyles? In: Stork, N. (ed), The Role of Ground Beetles in Ecological and Environmental Studies. Intercept, Andover, p.295-305.

Frankie, G.W., and L.E. Elher. 1978. Ecology of insects in urban environments. Annual Review of Entomology 23:367-387.

Gill D. and P. Bonnett. 1973. Nature in the urban landscape: a study of city ecosystems. York, Baltimore Maryland.

Gray J.S. 1989. Effects of environmental stress on species rich assemblages. Biological Journal of the Linnean Society 37:19-32.

Heliövaara, K., and R. Väisänen. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. Acta Forestalia Fennica 189:1-32.

Karr, J.R. 1998. Rivers as sentinels: Using the biology of rivers to guide landscape management. In: River Ecology and Management: Lessons From The Pacific Coastal Ecosystem. Springer, NY. P. 502-528.

Koivula, M., P. Punttila, Y. Haila and J. Niemelä. 1999. Leaf litter and small scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22:424-435.

Krebs, C.J. 1989. Ecological Methodology. Harper & Rowe, New York.

Lindroth, C.H. 1961-69. The Ground Beetles of Canada and Alaska. In 6 parts as supplements of Opuscula Entomologica, Part 1 supplement 35,p. I-XLVIII; Part 2 supplement 20, 1961, p. 1-200; Part 3 supplement 24, 1963, p. 201-408; Part 4 supplement 29, 1966, p. 409-648; Part 5 supplement 33, 1968, p. 649-944; Part 6 supplement 34, 1969, p. 945-1192.

Lövei, G.L., and K.D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology. 41:231-256.

Luff, M. 1996. Use of carabid beetles as environmental indicators in grasslands and cereals. Annales Zoologici Fennici 33:185-195.

Menshaka Jr., W.E. 1996. Vagility and the Florida distribution of the Cuban tree frog (*Osteopilus septentionalis*). Herpetological Review 27:37-40.

McDonnell M.J. and S.T.A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71:1232-1237.

McIntyre, N.E. 2000. Ecology of urban arthropods: a review and a call to action. Annals of the Entomological Society of America 93:825-836.

Moyle, P.B. 1986. Fish introductions into North America: patterns and ecological impact. In: Ecology of Biological Invasions of North America and Hawaii. Mooney, H.A. and J.A. Drake (eds), Springer-Verlag, New York, NY.

Niemelä, J.K. 1990. Spatial distribution of carabid beetles in the Southern Finnish taiga: the question of scale. In: Stork, N. (ed), The Role of Ground Beetles in Ecological and Environmental Studies. Intercept, Andover, p.143-155.

Niemelä, J.K. 1996. From systematics to conservation – carabidologists do it all. Annales Zoologici Fennici 33:1-4

Niemelä, J., D.J. Kotze, S. Venn, L. Penev, I. Stoyanov, J. Spence, D. Hartley, and E. Montes de Oca. 2002. Carabid beetles assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. Landscape Ecology 00: 1-17

Niemelä, J.K. and J.R. Spence. 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. Oikos 62:351-359.

Niemelä, J.K. and J.R. Spence. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. Ecography 17:166-175.

Niemelã, J.K. and J.R. Spence. 1999. Dynamics of local expansion by an introduced species: *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) in Alberta, Canada. Diversity and Distributions 5: 121-127.

Niemelã, J.K., J.R. Spence, and H. Cárcamo. 1997. Establishment and interactions of carabid populations: an experiment with native and introduced species. Ecography 20: 643-652.

Niemelã, J.K., J.R. Spence, and D.H. Spence. 1992. Habitat associations and seasonal activity of ground beetles (Coleoptera, Carabidae) in central Alberta. The Canadian Entomologist 124:521-540.

Nilsson, A.N., R.B. Pettersson, and G. Lemdahl. Macroptery in altitudinal specialists versus brachyptery in generalists-a paradox of alpine Scandinavian carabid beetles (Coleoptera: Carabidae). Journal of Biogeography 20:227-234.

Peters, T.M. 1977. The biology of invasions. In: Insect Ecology. Papers presented in the A.C. Hodson ecology lectures. Agricultural Experimental Station, University of Minnesota, Technical Bulletin 310, p. 56-72.

Pickett, S.T.A., M.L. Cadenasso, J.M. Grove, C.H. Nilon, R.V. Pouyat, W.C. Zipperer, and R.Costanza. 2001. Urban Ecological Systems: Linking Terrestrial, Ecological, Physical, and Socioeconomic Components of Metropolitan Areas. Annual Review of Ecology and Systematics 32:127-157.

Pielou, E.C. 1975. Ecological Diversity. Wiley-Interscience, New York.

Putman, R.J. 1996. Community Ecology. Chapman and Hall, London, UK.

Schaefer, M. 1980. Studies of arthropod fauna of green urban ecosystems. In: Urban Ecology, Bornkamm, R., J.A. Lee, and M.R.D. Seaward (eds.). Blackwell, London. P. 65-74.

Simberloff, D.S. 1972. Properties of rarefaction diversity measurement. American Naturalist 106:414-418.

Simberloff, D. 1986. Introduced insects: a biogeographic and systematic perspective. In: Ecology of Biological Invasions of North America and Hawaii. Mooney, H.A. and J.A. Drake (eds), Springer-Verlag, New York, NY.

Sit, V. and B.Taylor (ed.). 1998. Statistical Methods for Adaptive Management Studies. Research Branch, British Columbia Mining and Forestry, Research Branch, Victoria, British Columbia, Land Management Handbook No.42. pp.55-68.

Spence, J.R. 1990. Success of European carabid species in western Canada: preadaptation for synanthropy? In: Stork, N. (ed), The role of ground beetles in ecological and environmental studies. Intercept, Andover, p.129-141

Spence, J.R., D.W. Langor, J. Niemelä, H.A. Cárcamo, and C.R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. Annales Zoologici Fennici 33(1): 173-184.

Spence, J.R. and J.K. Niemelä. 1994. Sampling carabid beetle assemblages with pitfall traps: The madness and the method. The Canadian Entomologist 126:881-894.

Spence, J.R. and D.H. Spence. 1988. Of ground beetles and men: introduced species and the synanthropic fauna of western Canada. Memoirs of the Entomological Society of Canada 144:151-168.

Stork, N. 1990. The Role of Ground Beetles in Ecological and Environmental Studies. Intercept, Andover, UK.

Strueve-Kusenberg, R. 1980. Succession and trophic structure of soil animal communities in different suburban fallow areas. In: Urban Ecology, Bornkamm, R., J.A. Lee, and M.R.D. Seaward (eds.). Blackwell, London.

Ter Braak C.J.F. and I.C. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research 18:272-327.

Thiele, H.U. 1977. Carabid Beetles in Their Environments. Springer, Berlin.

Trojan, P. 1994. The shaping of diversity of invertebrate species in urban green spaces of Warsaw. Memorabilia Zoologica 49:167-174.

United Nations. 1993. World Population Prospects. United Nations, New York.

Wheater, C.P. 1988. Predator-prey size relationship in some Pterostichini. Coleopterists Bulletin 42:237-240.

White, C.S. and M.J. McDonnell. 1988. Nitrogen cycling processes and soil characteristics in an urban versus rural forest. Biogeochemistry 5:243-262.

APPENDIX 1

Table of Standardized Season Total Catch of Carabid Beetles in Aspen Forest in 1998 and 1999. Standardized season totals of trap catches per site in aspen. Full names of species can be found in Table 2.2 and site names in Table 2.1. Sites M1 and M7 were not used in the analysis and include only data from 1998.

Aspen	Sites											
Species	ML	MA	MC	L	RH	WM	ST	SH	M1	M7	BF	BG
C.nemoralis	287	257	319	74.3	34.1	28.3	0	0	0	0	0	0
C.granulatus	310	35.2	13.2	798	86.2	247	0	0	0	0	0	0
C.chamissonis	0	0	0	0	0	6.71	0	0	8.57	1.43	0	1
P.melanarius	5221	2077	1440	1600	1279	729	432	198	270	195	10.3	5.38
P.adstrictus	110	39.3	56.8	189	86	94.6	71.1	99	67.5	51.8	56.4	13.2
P.pensylvanicus	207	30.9	26.4	99	85.5	119	68	67.4	26.1	25.7	121	16.5
P.riparius	6	2.64	0.71	11.1	126	24.1	6	0	0	0	0	0
P.lugubris	0	0	0.86	0.71	0	0	1	0	0	0	0	0
C.ingratus	267	185	105	168	462	126	62.5	157	113	95.7	309	67.3
S.impunctatus	10	30.8	2.14	25.9	68.3	72.5	8.32	21.4	57.1	31.4	43.6	10.6
P.decentis	162	50	18.9	177	287	211	54	250	45.7	68.9	173	106
P.mannerheimi	0	0	0	0	0	0	0	0.86	14.3	1.43	1.43	1.57
A.retractum	35.7	25.9	22.8	32.4	54.9	129	16.4	66.7	22.1	7.5	36.7	21.1
A.picsolum	50	12.9	0	0	4.57	16.6	0.71	0	0	0	0	0
A.placidium	0	2.5	0.89	1	5.4	0.71	6.14	0	0	1.79	0	0
A.sordens	0	0	0	2	17.9	3.14	1	1.57	48.2	2.86	1.5	57.8
A.gratiosum	0.71	0	0	0	0.71	0	0.71	1.43	14.6	7.86	5.71	6.69
A.thoreyi	0	0	0	0	0	0	0.86	0.71	0	1.43	0	0
A.corvus	1.57	0	0.89	0.71	0	2.29	2.14	1.57	1.43	0	0	0.86
A.cupreum	0.71	0	0	0	0	0.86	0	0	0	0	0	0
A.superioris	0	0	0	0	0	0	0	0	10	1.79	0.89	0
A.propinquum	0	0	0	0	0	0	0	0	0	0	0.71	0
H.fulvilabris	2.43	4.07	8.64	5	16.1	12.1	3.14	6.32	0	2.86	10.4	0.71
H.ventralis	0	0	0	0	1.19	0	0	0	0	0	0	0
N.gyllenhali	13	0	0.86	4.71	0	6	0	0.86	0	0	0	0
S.marginatus	0	0	0	0	6.96	24.7	0	0	0	0	0	0
P.stygicus	0	0	0	0	7.71	3.43	0	3.43	1.43	3.57	1.43	3.57
P.foveocollis	0	0	1.61	0	0	0	0	4.29	4.29	1.79	0	5.18
P.septentrionis	0	0	0	0	0	0	1.57	12	4.29	1.79	3.29	22.8
P.lecontei	0	0	0	0	0	0	0	0	7.14	6.43	0	1.43
C.cribricollis	0	1.61	0	0	0	0	3.39	0	2.86	1.43	0	0.86
L.pilicornis	0	1.79	0	0	0	0	0.86	1.43	1.43	0	0.89	0
C.frigidum	0	0	0	0	0	2.57	1.43	0	10.4	4.64	0.71	0
C.alternatus	0.86	0	0	0	0	0	22.3	0	0	1.43	10.2	0
A.quenseli	0	0	0.71	0	0	0	0	0	0	0	0	0
A.cupreolata	0	2.43	0.86	0	0	0.86	0	0	0	0	0	0
A.hyperborea	0	0	0	0	0	0	0	0	1.43	0	0	0.71
C.fossor	0.71	0	0	0	0	0.71	0	0	0	0	0	0
B.lugubrius	0	0	0.86	0	0	0.86	0	0	3.21	0	0	0.71
T.apicalis	0	0	0.71	0	0.86	0	0.71	0	1.43	1.79	0	7.04
B.fortestriatum	0	0	0	0	0	0	0	0.86	0	0	0	9.46

APPENDIX 2

Table of Standardized Season Total Catch of Carabid Beetles in Grasslands in 2000. Standardized season totals of trap catches per site in grasslands. Full names of species can be found in Table 3.2 and site names in Table 3.1.

Grasslands	Sites											
Species	PRM	EDQ	SHW	VT	SUP	OXF	HLI	70	RG1	RG2	RG3	RG4
C.nemoralis	0	3.57	1.71	0	3.06	0	3.86	5.29	0	0	0	0
C.granulatus	0	56.6	5.14	0	31.7	3.57	0	2.57	0.86	2.2	3	4.71
P.melanarius	0	54	60.9	0	478	173	174	5.57	371	114	397	41
P.adstrictus	1	0	0	0	5.26	0	0	0	2.57	0	2.57	0
P.pensylvanicus	0	0	0	0	0.86	0	0	0	0.86	1	0.86	0
P.lucublandus	0	0.86	0.86	0	0.86	11.3	1.71	0.86	0	0	0	0.86
A. torrida	0	0.86	0.86	1.86	25.6	31	1.86	0	0	1	0.86	0
C.ingratus	0	0.86	0	0	4.57	0	0	0	8.14	0	11.4	20.6
S.impunctatus	0	0	0	0	2.06	0	0	0	0	0	0	0
A.cupreolata	1.71	2.86	2.57	0	11.7	2.86	32.1	0	1.71	0	1.71	3.43
A.quenseli	0	0	0	0	0	0	0	0	0	0	0	0
A.littoralis	0	0	0	0	1.86	0	1	0.86	5.14	0	0.86	0
A.ellipsis	0	1	0	0	9.97	2	4.86	0	0.86	0	1.71	0
A.placidium	0	0.86	0	0	2.57	1.2	0	0	0	0	1.71	0
A.sordens	0	0	0	0	0	0	0	0	1	0	1.71	1
A.retractum	0.86	0	0	0	0	0	0	0	0	0	0	0
A.cupreum	0	0	0.86	0	32.3	6.43	0	6.86	0.86	0	4.29	0
H.fulvilabris	2.71	0	0	0.86	1.71	1	0	0	6.57	1	1	0.86
P.foveocollis	0	0	0	0	0	0	0	0	0.86	1	2.57	0
C.cribricollis	0	0	0	0	0	2.2	0	0	0	4.71	0	0
B.obtusus	1.2	0	0	0	0	0	0	0	0	0	0	0
C.purpuricollis	0	0	0	0	0	0	1.71	0	0.86	0	0	0

APPENDIX 3

Table of Standardized Season Total Catch of Carabid Beetles in Graveyards in 2000. Standardized season totals of trap catches per site in graveyards. Full names of species can be found in Table 3.3 and site names in Table 3.1.

Graveyards	Sites											
Species	MTP	EDM	BCH	JWC	OLP	HLC	COL	LTM	BTH	LMT	SMK	SNC
C.nemoralis	0	0	2	5.14	0	0	0	0	0	0	0	0
C.granulatus	0	0	0	0	0	0	1	0	0	0	0	0
P.melanarius	0	18.4	20	6	2.57	14	30.6	1.86	336	0	0.86	3.71
P.adstrictus	0	0	2	0	0	0	0	0	0	0	0	0
P.pensylvanicus	0	0	0	0	0	0	0	0	1.71	0	1	0
P.lucublandus	0	0	0	0	0	0	0	0	0	0.86	0	1.86
C.ingratus	0	0	0	0	0	0	0	0	0.86	0	0	0.86
S.impunctatus	0	0	0	0	0	0	0	0	0	0	0.86	0
A.cupreolata	0	0	1	0	0	0	0	0	0	2.57	0	0
A.ellipsis	0	0	0	0	0	1	0	8.57	0	0	1	0
A.placidium	2	1	1	0	0	4.29	0	4.43	5.29	1.71	1	0
A.cupreum	0	0	0	0	21.4	30.1	0	0.86	9.57	0	3.86	0
H.fulvilabris	0	0	0	0	0	0	0	0.86	0	1.71	1.86	1.71
C.cribricollis	0	0	0	0	0	0	0	0	0	3.43	0	0
H.reversus	0	0	0	0	0	0	0	0	0	1.2	0	0